ASSOCIATIVE RESPONSES TO COLOUR AND PATTERN IN THE HUMAN VISUAL SYSTEM

by

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Dedication:

To my parents, Basil and Eleanor Wood

ABSTRACT

Psychophysical methods have been applied to the following four aspects of the McCollough effect with a view to the elucidation of its mechanism and its locus:

(1) time course of build-up and decay

(2) association of colour with scale of pattern

(3) interocular relations

(4) angular distribution function.

1. At normal light levels decay of the McCollough effect typically follows a power law with exponent $\approx -\frac{1}{3}$. Its growth follows a similar power law with exponent $+\frac{2}{3}$. In darkness decay is arrested. After a period in the dark the course of decay is similar to that immediately following exposure to the inducing stimuli. Unpatterned light is as effective as randomly patterned light in producing decay, but decay proceeds particularly rapidly during exposure to achromatic gratings at the same orientations as the inducing gratings.

2. A large pattern-contingent chromatic aftereffect can be induced and detected using stimuli which contain no straight oriented edges but which differ only in magnification or texture.

3. Although the McCollough effect transfers to a barely detectable degree to a covered or steadily illuminated eye, pattern-contingent chromatic aftereffects can be induced dichoptically, and can also have a specifically binocular component. The former are visible when each eye is tested separately, and are opposite in the two eyes, ("normal" in the eye exposed to coloured unpatterned fields, and "anomalous" in the eye exposed to achromatic patterns). The latter shows up as a difference between the strengths of effects seen monocularly and binocularly. This

difference is positive or negative according as the McCollough stimuli concurred or conflicted in the two eyes during induction of the effects.

4. The orientation contingent aftereffects induced by a single coloured grating have a Gaussian angular distribution function with points of inflection 42° apart and are of the complementary hue only. No signs of "opponent processing" of orthogonal orientations have been found. The nett aftereffect induced by successive exposures to two or more coloured gratings is the linear sum of the effects of the individual gratings.

It is suggested that these effects are best explained in terms of synaptic modification rather than fatigue of "edge-detectors".

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It is a pleasure to take this opportunity of thanking the many subjects who have patiently endured lengthy experiments, and also my family for their cheerful forbearance and support.

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CHAPTER 1 CONTINGENT AFTEREFFECTS

1.1 Introduction

Over the past 40 years a group of new visual aftereffects have been discovered (see table 1) whose existence strongly suggests that several parameters of our visual experience - among them colour, pattern and motion - are processed by the human visual system to some extent in combination.

Up to the mid-sixties, studies of the 'simple' negative aftereffects induced by exposure for a minute or two to coloured stimuli (or to moving, tilted, or periodic ones) had not indicated that more than one parameter was involved in each aftereffect. Thus the colour (or motion, tilt or spacing) of the inducing stimulus - together simply with its intensity and duration - appeared to determine the hue (or illusory motion, etc) seen as an aftereffect. But it has since become evident that after exposure to some pairs of the above parameters presented in conjunction, the strength of one or both of the two after effects induced depends upon the extent to which the second parameter is present in the test situation. Thus, when one has looked for a few minutes at a red field patterned with dots or bars of a uniform size and spacing, whilst all white surfaces afterwards appear tinged with green, those patterned with dots and bars of about the dimensions viewed during induction of the after effect appear greenest of all. The existence of a contingent aftereffect is most convincingly demonstrated if the aftereffect can be shown not merely to alter in strength, but actually to reverse in hue (or motion, tilt etc.) according simply to which test pattern is looked at.

Such a condition can be achieved by a fairly lengthy exposure to

table 1:
SOME CONTINGENT AFTER-EFFECTS
T indicates the parameter altered in the test situation.

		Colour	Contrast polarity	orientation	scale	direction of motion	stereoscopic depth	Duration
GIBSON	1933	chrom a-e	T					several hours
McCOLLOUGH	1965	chrom a-e		T				2-3 days
STROMEYER	mentioned by Harris 1970	chrom a-e			T			2 days
HEPLER	1968	chrom a-e				T		20 hours
HELD AND SHATTUCK	1971	T		tilt a-e				24 hours
VIRSU AND HAAPASALO	1973	T			spatial frequency a-e			-
FAVREAU, EMERSON, CORBALLIS MAYHEW AND ANSTIS	1972 1972	T				motion a-e		24 hours
MAYHEW AND ANSTIS	1972			T		motion a-e		10 minutes (VM)
WALKER	1972				T	motion a-e		7 hours (VM)
MAYHEW V. MACKAY	1973 1973 Appendix II		T			motion a-e		7 hours (VM)
WYATT	1974			tilt a-e	T			-
ANSTIS AND HARRIS	1974					motion a-e	T	5 - 40 minutes

two stimuli, presented alternately for a few seconds apiece in the same part of the visual field (fixation being unnecessary). Resuming the above example, if one wished to test whether after-effect hue can be contingent upon pattern magnification, a finely textured pattern and a coarser magnification of itself would be presented in red and green light respectively as the two stimuli. As a routine check, the pairing of texture and colour would be reversed upon another occasion under otherwise identical conditions and the aftereffect hues seen on coarse and fine test patterns again examined. Only if the aftereffects took approximately equal and opposite values on the two occasions could it be presumed that there was not some other process or bias producing the pattern-contingent change in aftereffect.

A general historical arrangement of the literature to about 1972 will be followed, with the aftereffects divided for clarity into two principal groups, those induced by stationary patterns and those induced by moving patterns. Brief references to microelectrode work on 'feature detectors' are included because of the notable influence which the findings have exerted on the discovery as well as the interpretation of the contingent aftereffects.

Apart from assuming that these effects share sufficiently strongly in several family likenesses for it to be appropriate to consider them side by side as in some sense a group, I have tried not to foreclose prematurely the question as to what mechanisms are responsible for these effects. In the next two chapters the experimental data which I have felt to be most significant are therefore reported as far as possible, without interpretation.

1.2 The prism aftereffect or 'Phantom' fringes*

The first indication from visual aftereffects of a degree of pairing of the processing of two parameters, - viz the polarity of the intensity step at an edge and the colour at the edge - came by chance from an experiment of J.J. Gibson's in 1931 (J.J. Gibson 1933, footnote 4) which was so fruitful in a number of ways that it is perhaps worth describing somewhat fully. In order to study the effect "on auditory and kinaesthetic space habits resulting from a 15° shift of the visual field" Gibson's student Miss Janet Goldstein for several days wore glass prisms before both eyes with their angle edges vertical and to the right. The prisms were unachromatised so simple refraction made all non-horizontal intensity steps appear to the wearer to be fringed by half the colours of the rainbow - the yellow to red colours on the right of every dark area, and the green to violet on its left. After 3 days of wearing the prisms Miss Goldstein reported that "this phenomenon... was less marked".** Much more astonishingly, when she finally on the fourth day removed the prism goggles she stated that "the colored bands were now seen with renewed vividness but that the effect was reversed, red now being on the left and blue on the right. The phenomenon persisted for several hours". This is the first reported example of what is now called a contingent aftereffect, the hue perceived being contingent in this case upon the presence and polarity of the intensity step at each dark/light boundary.

*The term 'fringe' has been applied to both the real edgings of refracted light in a spread of adjacent colours produced by the prisms and to the illusory edgings seen as an aftereffect; no reference to diffraction fringes is intended.)

**This was also observed by McFarland (1883) who says that after "a few weeks" of wearing 7° prisms "chromatism disappeared".

Although it is a negative aftereffect, the fact that both aftereffect hues - and neither - can be seen sequentially in the very same region of the subject's visual field according as various contrast edges and plain areas fall in that region means, as Gibson said, that "explanation cannot be made in terms of ordinary negative after-images".

It was not until 1947, when Ivo Kohler (1951, 1964) enthusiastically rediscoveredthis effect, that further properties of the illusory fringes were described and explanations for them sought. Kohler had been wearing prism goggles in an experiment similar to Gibson's for twelve days when he first removed the goggles and so noticed the aftereffect fringes:- "It* was as if the observer had developed the power of breaking white light into its components" - where the window frame met the night sky he saw a "yellowish red stripe" on the one edge and "bluish violet" on the other. Since "no known physiological or psychological factor" could produce such an effect he thought it possible that his eye lenses had become prism shaped during the 2 weeks of wearing goggles. So he used (1951, pp26,50) monochromatic (sodium) light to view contrast edges: further splitting of this by refraction is not possible, yet still he saw "in the region of every brightness difference... with or without goggles, the same coloured edges that (he) would have seen by daylight without the goggles". This left no doubt that the mechanism of these "subjective phantoms" must be sought within the nervous system.

Experiments by others besides Kohler over the following 20 years have brought out the following prominent quantitative properties of the "phantom fringes" which are suggestive as to the nature and site of this modification:-

*Kohler's writings and those of Hajos are translated from the German.

1.2.1 The Phantom fringe or prism aftereffect is a negative aftereffect.

1.2.2 It is very stable and is immediately visible on every dark/light boundary (except those exactly perpendicular to the line of the prism edge) (Kohler 1951, pp51,53). Whereas ordinary Hering afterimages fade, reappear and reverse with short time constants when one blinks, shifts ones gaze or turns the light on and off, Kohler describes the phantom fringes as doing none of these things, and as "distinguished by a quite exceptional stability".

1.2.3 Its time constant for reaching saturation is very long, being of the order of hours or possibly days as against the seconds or minutes which are typical of the many other visual negative aftereffects in which the motor system plays no part (see Table 2). When the wearing of 20 dioptre prisms was interrupted for an hour daily to determine the strength of the phantom fringes in terms of the real prism dispersion required to "cancel" them, it was found (in 6 subjects) that the aftereffect took over half a day of logarithmic growth to reach half its saturation strength, and about 10 days to attain the saturation level (Hay, Pick and Rosser, 1963). Hajos and Ritter (1965) in similar experiments (using in some runs one eye, and in others prisms producing opposite effects in the two eyes) obtained similar results:- over half the growth within the first day and saturation after 7-10 days. Prisms with 6.7 minutes of dispersion led to saturation values of about 5 minutes of arc. Kohler made no measurements of the growth of the effects generated by his 15° prisms, but judging from his account of the aftereffects' power to render the real fringes totally invisible at first only by very dim illumination, but later at a black and white movie, it seems to have been still growing between the 16th and 50th days of continuous prism wearing. The inducing stimulus

Table 2. Some Properties of several after effects of viewing colour and/or pattern

Aftereffect	Time to reach saturation strength	Source of data	Time to disappear	Source of data	Interocular Transfer	Source of data	Angular distribution of effect	Source of data	Spatial frequency dependence	Source of data
(ordinary) chromatic a-e	5 min (using 8mlm) (for induction)	own observation	80 min (following 10 min induction)	Own observation	Without effect in other eye Not without effect in other eye	Crook 1930 Bocci 1896	-	-	-	-
positive after-images	4 sec (using $2x10^6$ Td for induction)	Padgham 1957, 1968	140 sec up to 7 min ($4x10^5$L)	Padgham 1957, 1968 Norma Miller, 1966	-	-	-	-	-	-
the 'complementary' image	15 - 20 sec 20 sec	Purkinje 1823 Wilson 1960	briefer than induction 6 sec (at 1 log ft L)	Purkinje 1823 Wilson 1960	Stronger with binocular stimulation. Some important aspects of the effect are absent using dichoptic stimulation by pattern and noise fields	Wilson 1960 MacKay 1978	a-e is principally seen running at 60-120° to the stimulus lines. No meridional differences	Purkinje 1823 MacKay 1957	peaks at .05 c/cycle i.e. .35 cycles/ degree	Wilson 1960
a figural aftereffect in which a short black line repels a similar parallel line	1 min: 20 sec to ½ strength	Hammer 1949	90 sec: ½ life 30 sec following 2 min induction	Hammer 1949	-	-	-	-	-	-
curvature	10 min but most of growth by 45-90 sec >4 min; 1 min to ½ strength	Gibson 1933 Ikeda and Obonai 1957	>60 sec following 5 min induction 3 days following 12 days induction exponential decay from a single initial strength. Half life — Induction time 2 sec — 1 sec 4 sec — ½ min 12 sec — 1 min 24 sec — 5 min	Bales and Follansbee 1935 Hajos and Ritter 1965 Ikeda, Hisako and Obonai 1953	56%	Gibson 1933	a-e at all orientations of curve	Gibson 1933	-	-
tilt aftereffect	1½° tilt after 45-100 sec. 2° tilt after 18 msec 3½° tilt after 20 sec	Gibson and Radner 1937 Sekuler and Littlejohn 1974 Campbell and Maffei 1971	5 min following 10 min induction	Vernon 1934	100% (colour specificity lost in transfer)	Campbell and Maffei 1971 (Lovegrove and Over 1973	Largest effect when test lines at 8° to inducing lines. Strong (50%) secondary maximum at about 80° to inducing stimulus. No meridional differences	Gibson and Radner 1937 Campbell and Maffei 1971 Mitchell and Muir 1976	a-e independent of test spatial frequency	Parker 1972 Campbell and Maffei 1971
large tilt effect learned only during walking	½ - 2 hours above 48 min	Mikaelian and Held 1964 Ebenholtz 1966 Redding 1975	56 min following 48 min induction ½ life 12 min	Redding 1975	65%	Ebenholtz 1966	-	-	-	-
reduction in visibility of grating	5 sec (using frequency of seeing as measure) 60 sec (using threshold measure)	Gilinsky 1968 Blakemore and Campbell 1969b	11 sec following 5 sec induction 60 " " 60 " " 30 min " 60 min " 2 hrs " 30-90 " "	Gilinsky 1968 Blakemore and Campbell 1969b Heggellund and Hohmann 1976 Meccacci and Spinelli 1976	62%	Blakemore and Campbell 1969b	No effect beyond 35° falls to ½ strength at 6¼° No meridional differences	Blakemore and Nachmias 1971 Gilinsky and Mayo 1971 Hirsch, Schneider and Vitiello 1974	maximum effect when test matches adapting frequency and for 3-14 cycles/degree. bandwidth 1 octave	Blakemore and Campbell 1969b
reduction of evoked potential by viewing grating	about 30 min	Meccacci and Spinelli 1976	20 min following 30-90 min induction	Meccacci and Spinelli 1976	-	-	-	-	-	-
spatial frequency shift	2 min	Blakemore, Nachmias and Sutton 1970	more than 8 min following 6 min induction 160 min following 30 min induction	Blakemore, Nachmias and Sutton 1970	67%	Blakemore, Nachmias and Sutton 1970	No effect beyond 35° ½ strength at 6¼°	Blakemore, Nachmias and Sutton 1971	no effect 2 octaves away from inducing spatial frequencies	Blakemore, Nachmias and Sutton 1970
aftereffect of seen motion	80 - 100 sec.	Holland 1957	8-18 sec following 15 sec induction 22 " " 2 min " 4 min following 5 min induction	Holland 1957 Holland 1965 Taylor 1963a	70% 52% - 76% (depending on input to non-exposed eye)	Holland 1957 Lehmkuhle and Fox 1976	no effect on duration in perpendicular direction	Wohlgemuth 1911	18 cycles/degree more effective than 9 cycles/degree	Wohlgemuth 1911
'phantom' fringe or prism a-e	8 - 14 days	Hay, Pick and Rosser 1963 Hajos and Ritter 1965	4-12 days following 14-50 days induction	Hay, Pick and Rosser 1963 Hajos and Ritter 1965 Kohler 1951	none	Hajos and Ritter 1965	no effect at perpendicular orientation ½ width 35-60°	Kohler 1951 own observations	maximum when test matches adapting frequency; strongest at 1 cycle/degree	Stromeyer, Lange and Ganz 1973
McCollough effect	30-90 min	Stromeyer 1971 Riggs, White and Eimas 1974	1½ - 7 days following 10-20 min induction	Riggs, White and Eimas 1974 MacKay and MacKay 1975	none	McCollough 1965 Stromeyer 1972b Murch 1972	no obvious meridional differences a-e falls to ½ strength at 22°	Fidell 1970 Hajos 1970 MacKay and MacKay 1977	maximum when test matches adapting frequency and for 5-10 cycles/ degree	Stromeyer 1972 Lovegrove and Over 1972

provided by the normal environment may be far from optimal in the luminance, quantity and orientations of the contrast borders it provides. I have found, however, that a well-lit* black and white grating viewed through 20° prisms with stationary head for 2 hours resulted only in a faintly visible aftereffect which bore no comparison with Kohler's account (on day 16) of "colours as of costly stained glass - by fluorescent illumination". There seems little doubt then, that as the above literature indicates, the time constant for the growth of the prism aftereffect is several hours.

1.2.4 Its time constant of decay is also long. Janet Goldstein (J.J. Gibson, 1933) found that following 45 waking hours of wearing the prism goggles the aftereffect lasted "several hours". Hay, Pick and Rosser (1963) after ten days of prism wearing found that 4/5 of the decay occurred during the first day but that the effect was still measurable for up to 4 days. Hajos and Ritter's graphs tell a similar story. Kohler, on day 17, mentions that he can "sleep all night without (the fringes) disappearing" and when he terminated the prism wearing after 50 days found that the phantom fringes took 12 days to fall to the "barely visible" level.

1.2.5 The effect is dependent upon test contrast. The phantom fringes are not seen if there is no luminance step between adjacent differently coloured areas (Kohler, p53). The strength of the fringes is directly proportional to the luminance ratio of the test boundary. This was

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* 86 cd/m^2 white stripes

inferred by Hay, Pick and Rosser (1963) from their finding that their subjects chose the same prism to cancel their phantom fringes for all luminance ratios of two uniformly illuminated half fields. Since the strength of the real fringes produced by the cancelling prism is proportional to the relative luminance of the two fields, it is deduced that an effect which exactly keeps step with them must also be so. Hajos and Ritter (1965) have confirmed the finding.

1.2.6 Dependence upon test luminance. Kohler repeatedly remarks that the fringes seen without the goggles were the more "colourful and definite, the dimmer the test situation". At scotopic light levels, however, they were not visible (Kohler 1951; Hay, Pick and Rosser, 1963, see 2.4.7)

1.2.7 The effect is monocular. When subjects wore a prism in front of one eye and an occluder on the other for 13 days, two other effects produced by the prisms - viz curvature of straight lines and a change of eye-hand coordination - transferred strongly to the occluded eye, but the phantom fringes did not (Hajos and Ritter 1965). When prisms were worn in front of both eyes but with their angles pointing opposite ways, the phantom fringes measured after 8-14 days were oppositely coloured in the two eyes and as strong on the same test field as they had been following monocular induction (Hajos and Ritter, 1965).

1.2.8 The fringes can be seen at up to 30° from the fovea (Kohler, 1951).

1.2.9 Finally a curious observation of Kohler's (p53) should not be omitted though it perhaps tells more about ordinary chromatic afterimages than about phantom fringes. He says that fixation (presumably without his prisms) produced shortlived Hering negative after images as if the contrast edges observed had "really been coloured" (Kohler, 1951).

1.3 Explanations of the Phantom fringes

Explanations of the above effects have been offered in various widely differing, though not necessarily conflicting, terms. Kohler (1951, 1962) made the practical point that the aftereffect would, on average render invisible any fairly permanent chromatic aberrations generated by the eye and by spectacles. Gibson (1968) includes this effect among the negative aftereffects which he saw as evidence that a process of 'normalisation' operates along many perceptual dimensions. His persuasive thesis (1937, 1968) was that our perceptual systems are not preset as to their working range, but adjust and update, deriving their ongoing norms for qualities like 'whiteness', 'straightness' from the average of signals recently received from the environment*. Attention has been drawn to the memory-like durations of this and other contingent effects, and the idea explored that the now numerous family of contingent aftereffects are learned associations (e.g. "unconscious learning" Kohler, 1951; Murch, 1976; Mayhew and Anstis, 1972). In 1965 Celeste McCollough (see below) suggested a mechanism for the effect in terms of the properties of single nerve cells, and it is this type of physiological approach which has held the centre of the stage ever since.

1.4 The 'edge-detector' explanation of phantom fringes

The fatiguing of single units had already been advanced (Barlow and Hill, 1963b) as an explanation for another negative perceptual aftereffect - the waterfall effect. Barlow and Hill (1963a) had observed that when a black and white random pattern was moved continuously in one direction in

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* D.P. Andrews (1964) is a source for further theoretical work of a similar kind, in particular that of H. Helson (1938-1948).

front of a rabbit's eye, those ganglion cells in its retina which responded to this direction of movement were rendered less responsive by the prolonged stimulation and remained temporarily (for ½-2 min) less active than normal even when stimulation ceased; whereas neighbouring motion-sensitive cells which had been unresponsive to the stimulus while it moved in that particular direction, maintained a steady level of 'resting discharge' totally unaffected by the movement or cessation of movement of the stimulus. Barlow and Hill (1963b) suggested that the perceptual effects in humans might be accounted for in terms of the resulting temporary imbalance of activity in the population of movement sensitive cells.

Hubel and Wiesel's discovery (1962) of cells in the cat cortex sensitive to the polarity and orientation of a dark/light border led McCollough (1965b) to propose a similar selective adaptation to account for the phantom fringes. Her explanation involves the two assumptions that "edge detector" systems in humans have some degree of spectral selectivity, and are "adaptable". "Neurophysiological work shows that edge-detector systems are orientation-specific: a vertical boundary with the light side to the right is detected by one system while another vertical boundary with the light side to the left is detected by another. It seems not unlikely that the phantoms are to be explained by the adaptation of one system to yellow, the other system to blue". Hubel and Wiesel had not at this stage investigated the colour sensitivity of the cortical cells they described (as they were working on the cat which has poor colour vision). But colour opponent cells (without orientational properties) were becoming known in both LGN (De Valois, Jacobs and Jones, 1963; Wiesel and Hubel, 1966) and cortex (Motokawa, Tiara and Okuda, 1962) of the rhesus monkey, and later a modest proportion were found in its striate cortex having both orientational and chromatic preferences:- 12/177 complex, largely extra-foveal cells, Hubel and Wiesel, 1968; 12/122 colour opponent cells, Dow and Gouras, 1973; 30% of 73 cells having colour preferences, Bertulis, Guld and Lennox-Buchtal, 1977.* McCollough's assumption that cells might exist in humans sensitive to both orientation and colour therefore seemed well within the possibilities. The strong monocularity of the phantom fringes presented something of a problem, for few of the orientationally sensitive cells described in the cat and monkey cortices were exclusively monocular (e.g. Dow and Gouras, 1973 and Hubel and Wiesel, 1962, who state that of 233 cells 84% were to some extent influenced by inputs from the two eyes). McCollough therefore presumed that the edge detectors involved in the phantom fringes (and in the McCollough effect) "must be located below the convergence of inputs from the two eyes".

The sharpness of the angular tuning of the cells described by Hubel and Wiesel (1962) led McCollough to propose a new inducing stimulus, which though of a similar form to the prism fringes, proved conspicuously more effective in generating an after effect. Since "edge-detector systems" differ not only in polarity but are also highly sensitive to preferred angle of tilt of the border, she reasoned that it should be possible to demonstrate differential adaptation of horizontal and vertical "edge-detector mechanisms".

1.5 Colour contingent upon orientation: The McCollough effect.

McCollough (1965b) accordingly tried the experiment of edging contrast borders (of both polarities) at two widely separated orientations with different colours: subjects viewed - without fixation - an alternation on a projection screen of a vertical orange and black grating with an otherwise identical horizontal blue and black grating (each slide was presented for

*Zeki, however, (personal communication March 1976) has emphasised that he has never found an orientationally sensitive cell with colour opponent properties - in the sense of giving an 'on' response to one range of wavelengths and an 'off' response to another.

5 sec. followed by 1 sec. of darkness). After as little as 2-4 min, subjects shown a white test card on which black horizontal and vertical lines had been ruled in two separate areas, reported a "blue-green" coloration of the area with vertical lines and "orange" on the region with the vertical lines. "Although the colors are not as saturated as ordinary negative after-images, the two halves are clearly of different hue". "When either the head or the test field was turned through 90° the colors changed places", and when the pattern was in an oblique position at 45° "all color disappeared". Thus though the same area of the subject's retina had presumably been equally exposed to two complementary colours, a negative aftereffect had developed, contingent upon the presence and orientation (relative to the head, or more probably, the retina, Ellis, 1976), of the test gratings. McCollough's control experiment in which the stripes were omitted from the coloured inducing slides produced no chromatic aftereffect.

Feeling that this new effect, though so much more rapidly induced, was allied to the phantom fringes, McCollough checked that like them her effect (1) was clearly visible by monochromatic light, (2) became stronger with a longer induction period, (3) was slow in disappearing, "persisting for an hour or more" after a "few minutes" exposure, (4) did not show interocular transfer after 2-4 min exposure of one eye, and could be simultaneously induced of opposite hues in the two eyes for the same test pattern orientation by presenting opposite pairings of orientation and colour to the two eyes during induction. She concludes that "these observations strengthen the supposition that chromatic fringe adaptation... is explainable as colour adaptation of oppositely oriented... edge-detector systems".

Over the succeeding ten years, although further properties of the McCollough effect have been studied, very little has emerged either to strengthen or dismiss this tentative equation of the origins of the McCollough and prism aftereffects. As table 2 shows, their angular spread functions are both broad, and the forms of their time courses for decay not dissimilar; only* between the induction times they take to reach half strength is there a notable difference (15 min and 6 hours resp.). This may be because a maximally efficient "prism" stimulus has not yet been devised. It is perhaps also a difference to be expected if the types of cell described by Hubel and Wiesel (1962) are indeed involved in the two aftereffects, for the McCollough stimulus of gratings will affect the bar sensitive cells in addition to the edge sensitive ones. Alternatively it may indicate that the spatially repetitive aspect of the McCollough stimulus is more important than the orientational part (7.1)

Several further properties of the McCollough effect are summarised below. Some other properties are dealt with in chapter 2 in greater detail and also in the rest of this thesis.

1.5.1 <u>The McCollough Effect: inducing stimuli and test variables</u>

1.5.1.1 Timing of stimulus presentation. McCollough used alternate brief (5 sec) equal presentations of two gratings in complementary colours in order to emphasise that simple chromatic aftereffects were not responsible for her aftereffect. The conditions she chose are in fact about optimal for producing an effect (Keith White, unpublished thesis 1976b), but rhythmical alternation of two stimuli is not essential. Continuous unfixated viewing of a single coloured grating (Stromeyer, 1969; Hajos, 1970), or of a 'rainstorm' of red and green slits at two orientations on a black ground (VM unpub.) also give good aftereffects. Gratings flashed repeatedly even at extremely short durations (10^6 cd at 60 μsec, Stromeyer and Dawson 1974) produce an aftereffect but stabilised images of the

*see also 2.4.8 on visibility at scotopic levels of illumination coloured gratings do not (Leppman and Piggins, 1973).

1.5.1.2 The colours which can induce McCollough aftereffects are not limited to any part of the visual range, though reddish and greenish stimuli produce detectable aftereffects most rapidly (Stromeyer, 1969, 1972a; Hajos, 1967). Aftereffects have been reported on test fields like McCollough's, following exposures to pairs of gratings whose non-black stripes were blue and orange (Corning 5-56, 2-73 resp. and Wratten 44A, 25 resp., McCollough 1965), red and green (Hajos, 1967), yellow 588 nm and green 547 nm, blue 440 nm and green 547 nm (Hajos, 1970), red and yellow (McCollough and Clark, unpub. quoted by Hirsch and Murch, 1972) and even red and white, or green and white (Murch and Hirsch, 1972).

A single black and white grating viewed alternately with an unpatterned coloured field also gives an aftereffect, but of the same hue as the coloured inducing field - as if induced by the simple negative aftereffect (see section 2.9.6 , Murch and Hirsch, 1972). When the interval between presentation of the patterned and coloured stimuli is lengthened to 50sec this aftereffect is much reduced in strength.

If, following induction of an aftereffect by means of red and green orthogonal gratings, the gratings are both turned through 90° and a second McCollough exposure presented, the aftereffect is rapidly reduced, passes through neutral and reverses (Hajos, 1967).

1.5.1.3 Contrast. Inducing gratings in which the non-coloured stripes are not black but grey of the same luminance as the coloured stripes produce no aftereffects. Gratings with white and coloured stripes produce aftereffects of the same hues as black and coloured gratings but much weaker (Harris and Barkow, 1969).

1.5.1.4 Continuous contours. It is not essential that the contours of test or inducing stimuli should be continuous straight edges; 'stripes' made up of rows of circular 40' diam discs on a black ground proved only 15% less effective a stimulus than gratings. The discs were 0·2° and 1.5° apart in two directions at right angles (Hajos, 1967). Nor are crisp contours required: the test gratings may be blurred (Harris and Gibson 1968b), or serrated at 45° with 1/5° steps (May and Matteson, 1976) without much loss of the coloured effects.

1.5.1.5 Retinal specificity. Opposite aftereffects were induced "simultaneously in adjacent retinal regions" (to left and right of a fixation point) by presenting opposite pairings of colour and orientation of the gratings in the two regions of the visual field (Harris 1969).

1.5.1.6 Angular dependence of the effect. The angular spread of the aftereffect is broad: the pink aftereffect seen upon a single vertical achromatic grating after viewing a vertical green and black grating fell to about half strength when the test grating was turned to 22° to the vertical (Hajos, 1970). When a pair of coloured inducing gratings are used it is not necessary that they should be at right angles to each other; effects, though weaker, were obtained down to angles of 20° between the inducing (and test) gratings (Fidell, 1970). Nor is it necessary that inducing gratings should be horizontal and vertical: aftereffects of roughly similar strength were obtained with inducing and test gratings turned through 45° (Fidell, 1970).

1.5.1.7 Pattern spacing. The use of uniformly spaced parallel lines to induce and test for a McCollough effect introduced an ingredient in this aftereffect which had not been noticeably* present in the prism aftereffect. There is, in the McCollough effect, an association not only of colour and orientation but also of colour and some aspect of the pattern subtense or spacing. An audience (Harris, 1970) seated at various distances from the projection screen during presentation of the coloured gratings were invited to view test gratings of the same spacing while walking about the room. They found that the aftereffect hues altered in intensity with distance from the screen and were strongest for each person when he returned to his original place. Using "coarse, medium and fine" gratings all viewed from one distance, Teft and Clarke (1968) also concluded that the strongest effects were obtained when induction and test gratings were of the same spacing. The remarkable feature of both these experiments is that the more distant or finer grained test grating, though it provides a greater number of suitably oriented stimuli on a given part of the retina, nevertheless produces a smaller chromatic effect than the test grating whose spacing matches that of the inducing grating.

1.6 Colour contingent upon grating spacing

The spatial aspect of the McCollough effect raised the question as to whether a chromatic aftereffect could be induced in which the illusory hue of achromatic gratings would be contingent upon the texture of the test grating. Stromeyer was the first (Harris, 1970, mentions a personal communication of 1969) to demonstrate such an effect. "After prolonged adaptation to wide red stripes and narrow green ones (both vertical), subjects saw differently coloured aftereffects on wide and narrow test

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* Stromeyer, Lange and Ganz (1973) have since reported spatial frequency sensitivity, with a maximum at 1 c/d, in a chromatic aftereffect contingent upon the polarity of contrast of a venetian-blind like pattern with a saw tooth luminance profile.

stripes —"green on wide and pink on narrow".

Like the McCollough effect this chromatic aftereffect contingent on grating spacing is long lasting and does not show interocular transfer (VM unpub.) Reports as to its angular spread were conflicting; Leppman's (1973) subjects reported that "the aftereffect strengths were similar" on test fields oriented parallel to and perpendicular to the two vertical inducing gratings, whereas Lovegrove and Over (1972 footnote 9) said that "colour aftereffects could not be generated under these (perpendicular testing) conditions".

In accord with the experiments of Harris (1970) and of Teft and Clark (1968) (mentioned above) on the McCollough effect, the chromatic aftereffect contingent upon the spacing of vertical gratings was found to look strongest on test gratings whose spacing matched that of the inducing grating (Stromeyer 1972b) or gratings (Lovegrove and Over, 1972) for grating spacings of 1-20c/degree. The largest effects were generated, in a given time, by red and by green gratings of about 5-10c/degree. The observed fall-off of the effect below 5/degree is probably exaggerated by the fact that the total number of contrast edges presented to the subject in the broadly striped portions of the test field was small (only six stripes at 1 cycle/degree for both the above papers). The tuning curve is similar for all inducing spatial frequencies from 1-20c/degree, being symmetrical about the maximum on a logarithmic scale and broad with a total width of about 1-2 octaves at half strength (Stromeyer, 1972b; Lovegrove and Over, 1972; Breitmeyer and Cooper, 1972).

With test gratings at various distances in a lighted room so that 'size constancy' could operate, Harris (1970, 1971) concluded that the aftereffect strength depended upon the retinal angular subtense rather than upon the perceived width of the stripes. Stromeyer (1972b) has, however made the interesting observation that two test gratings which are identical in all respects can take on different hues appropriate to the illusory spacings induced by viewing a Blakemore and Sutton figure of appropriate dimensions. When the subject had previously been binocularly exposed for 15 min to red and green vertical gratings of a broader and a narrower spacing, this chromatic effect was seen only by the eye which had viewed Blakemore and Sutton's inducing figure and did not transfer though of course the spatial frequency shift did. Stromeyer thinks this lack of transfer may indicate that the site of the McCollough effect precedes the site of the interocular transfer of the spatial frequency shift.

1.7 The relation of the spacing-contingent chromatic aftereffect to achromatic effects involving spatial frequency

At about the time of Stromeyer's discovery of the above chromatic aftereffect contingent upon grating spacing, other workers were finding that spacing was an intersting variable in both psychophysical (Pantle and Sekuler, 1968; Campbell and Robson, 1968; Blakemore and Campbell, 1969a,b) and in single unit experiments (Campbell, Cooper and Enroth-Cugell, 1969), in each case using achromatic gratings. It was suggested (by Breitmeyer and Cooper, 1972 and Lovegrove and Over, 1972) that the same "spatial frequency analysers" were being adapted by both the chromatic and the achromatic exposures. The bandwidths yielded by the psychophysical experiments were certainly similar. There were even signs in the chromatic experiments of the "lowest spatial frequency channel" at 3 cycles per degree which had already been encountered in the achromatic masking experiments of Blakemore and Campbell (1969a,b). Though this last feature may be largely an artefact of the narrow (1.5°) test fields and consequent small number of grating cycles used in these experiments (cf. Tolhurst 1973 and Stromeyer 1972b), it could still be contended that under rather similar experimental conditions, similar spatial frequency characteristics were obtained from the achromatic and chromatic studies.

The diversity, however, which was rapidly apparent in the time constants and other properties of various aftereffects involving gratings (see table 2 for summary) made it clear by 1973 that they could not all be evidences of the same adaptation of the very same 'detectors'. Two demonstrations involving the spatial frequency shift pointed up its distinctness from chromatic aftereffects. The first concerns interocular transfer and the second colour specificity. Murch (1972) presented Blakemore and Sutton's inducing figure alternately vertically and horizontally in red and green light respectively to one eye for a total of 16 min and found that though the spatial frequency shift transferred to the other eye the chromatic effects contingent upon orientation were seen only by the exposed eye. Two possible explanations were advanced for this, and for the similar situations in tilt a-e and motion a-e where colour information does not transfer (Over, Long and Lovegrove, 1973; Over and Lovegrove, 1972): (a) that "binocularly driven spatial detectors are insensitive to colour", (Over, Long and Lovegrove, 1972; Coltheart, 1971) and (b) that "the McCollough effect arises as a result of adaptation of opponent process color receptors located in the LGN which feed into orientation-sensitive units in the cortex" (Murch, 1972). The first of these explanations takes it for granted that the 'detectors' in the monocular pathway are colour sensitive, but a qualitative demonstration by Virsu and Haapasalo (1973) cast doubt on whether this was so for the monocular mechanism involved in the spatial frequency shift; following a

15 min presentation of Blakemore and Sutton's inducing stimulus in red light, the spatial frequency shift was observed on red, green and blue test gratings and "was not noticeably weaker on any colour of test gratings". The colour filters used had not been so selected as to excite particular colour channels exclusively, but Drs Campbell and Cavonius are referred to as having made (unpublished) observations of the spatial frequency shift even "when the effects of adaptation and test gratings are restricted to different π mechanisms."

In summary, the relation between the processing of achromatic and coloured gratings is not so simple as was at first anticipated and it seems unlikely that the same colour-coded orientation and spatial frequency sensitive units can be responsible for all the effects observed.

1.8 'Spatial frequency' or some other function of pattern spacing?

A one-dimensional grating with a sinusoidal luminance profile is a particularly simple pattern to specify mathematically. The idea that the visual system also treats it as basic, and performs spatial Fourier analyses of the incoming two-dimensional patterns of light in a fashion analogous to the ear's supposed time analysis of air pressure patterns has been proposed (Blakemore and Campbell, 1969b; Blakemore and Nachmias, 1971) and has been influential. It has come under fire, however, on various grounds, largely concerned with the fact that Fourier analysis presupposes linear addition whereas the response of the eye's receptors to increasing intensity is logarithmic (Maudarbocus and Ruddock, 1973 b; Burton, 1973; Henning, Hertz and Broadbent, 1975; Fiorentini, Sireteanu and Spinelli, 1976). Nevertheless, though spatial frequency may not be the commodity which the nervous system processes, the existence of the spatial frequency shift (Blakemore and Sutton, 1969), simultaneous spatial frequency contrast (MacKay, 1973) and the chromatic aftereffect contingent upon pattern spacing show that some aspect of the coarseness, texture density or 'blob' size of a repetitive pattern is. Indeed it had been emphasised by J.J. Gibson (1950) many years before that texture density is one of the most basic features of the visual array around us, by means of which we apprehend the angle which surfaces make to our line of sight and detect our own motion in the world as well as the relative motions of other objects.

Experiments have been performed on the McCollough effect (Uhlarik and Osgood, 1974) and on the spatial frequency shift (Burton, Nagshineh and Ruddock, 1977) to determine in each case whether it is the spatial frequency, the width of the black bars or the width of the white bars which determines the aftereffect strength. Both conclude that their results cannot be explained in terms purely of spatial frequency.

For the experiment on the McCollough effect, a set of gratings having various ratios of the widths of the black to the coloured or white bars was employed both in inducing and in testing the aftereffects. After a 12 minute McCollough exposure to red and green vertical and horizontal gratings of a particular ratio, the subject was shown a large montage of abutting achromatic gratings having various widths of either the black or the white bars and was asked to select those on which he saw the strongest hues. The performance of the experiment by Uhlarik and Osgood (1974) is open to criticism on a number of scores, in particular the needlessly small extent (4°x6°) of the inducing field relative both to the widths (5/6°) of the broadest bars and the test field (about 10°x25°). Nevertheless it does seem clear from their results that a pattern and its photographic negative are not treated as equivalent by the McCollough mechanism although they have identical spatial frequencies. The authors' conclusion is that the width of the black bars matters but not that of the white.

1.9 A one to one correspondence between aftereffects and single cortical cells?

When Hubel and Wiesel in 1968 found a small number of 'complex' cells sensitive to both orientation and colour, McCollough's prediction, that units with such properties might exist, seemed nicely fulfilled. Whether such cells have the monocularity and the long recovery times appropriate to the McCollough effect has not been determined. Nevertheless the attractive simplicity of this possible link between neurophysiology and perception caught the imagination and acted as a spur to further investigations. Taking as starting point the reports of cells sensitive to other 'features' of the visual world such as curvature (Lettvin, Maturana, McCulloch and Pitts, 1959), direction of motion (Lettvin et al, 1959; Barlow and Hill, 1963a) and the width (Hubel and Wiesel, 1962) and length (Hubel and Wiesel, 1968) of bar stimuli, the eager hunt was on for further perceptual phenomena which might correspond to adaptation of other colour-coded "feature detectors". Harris (1968) lists a flutter of doctoral theses and personal communications in 1966-8: Mary Viola was unable to produce a 'curvature effect', Celeste McCollough (1967) produced 'a motion effect', Sorenson (1967) found a line 'spacing effect', and Linda Fidell (1968) tried without success to produce a 'line length' effect. (It should be mentioned that curvature has since been reinvestigated and though positive results were claimed by Riggs 1973 and White and Riggs 1974, negative ones were reported by Stromeyer and Riggs, 1974; MacKay and MacKay, 1974; and Sigel and Nachmias, 1975 under more tightly controlled conditions; see ch 3.2.7). This degree of success in pairing off cells and aftereffects was encouraging - but it also began to suggest that if such cells are 'pre-set' in their sensitivities a rather large number of cells must be allocated to each area of the retina to cover combined sensitivities in so many dimensions.

Harris and Gibson (1968a,b) and Harris (1972) suggested that neural machinery much cruder* than the highly fastidious cortical cells, could adequately and much more economically explain the observed contingent aftereffects. The minimal requirement (Gibson and Harris, 1968) is a population of fatiguable units, each with inputs from a pair of non-coincident areas of the retina and having some variation of wavelength sensitivity among the total population. This "dipole" theory still hangs on the adaptation or fatiguing of single units, but it does permit the site of these units to be peripheral to the more sophisticated later stages of pattern and motion analysis. On such a theory the several respects in which the properties of contingent aftereffects differ from those of cortical cells fall into place. Unlike cortical cells the McCollough effect is insensitive to small scale pattern detail and depends rather upon overall orientation or spacing (May and Matteson, 1976). It is, however, sensitive to pattern contrast. Though there are known to be cortical cells sensitive to complex features such as curvature and line length, it is significant, Harris and Gibson suggest, that corresponding contingent aftereffects have not been found.

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* The bluntness of the mechanism which is revealed by adaptation compared with that revealed by straightforward perception is remarked on also, (though without similar conclusion) by Blakemore, Nachmias and Sutton 1970; "It" (the hypothesis that there is in humans a lowest spatial frequency channel at 3 cycles per degree)"is a very perplexing hypothesis because one can clearly detect... and easily discriminate... patterns far below 3 cycles per degree."

As the number of known contingent aftereffects has swelled over the past ten years and their long durations have been appreciated a growing number of others besides Gibson and Harris have expressed dissatisfaction with the notion that each new aftereffect is evidence of the fatigue of yet another double or (treble) duty feature detecting cell (e.g. Mayhew and Anstis 1972; Murch 1972; Favreau 1976b); but for many years theirs was a lone and unfashionable voice.

1.10 Apparent orientation contingent upon colour

In 1971 Held and Shattuck reported an aftereffect which may be a converse of McCollough's. Following a 10 min McCollough-style exposure to an alternation of a red and a green (Wratten 55,26) grating tilted respectively at 10° to left and to right of the vertical, a vertical grating whose upper and lower halves were lit by red and by green light resp, appeared bent by about ½°, the angle pointing towards the left; that is, the apparent orientation of a grating was very slightly different according as it was lit by red and by green light. This very small effect was measured by showing subjects a set of 9 gratings which were genuinely 'kneed' along the horizontal dividing line between red and green by angles of from 1.5° to the left to 1.5° to the right and asking them to report of each grating whether it appeared to point left or right; the test slides were presented for 2 sec apiece 10 times in increasing and decreasing order. The angle which a subject judged left-pointing upon 50% of trials was taken to be perceived as straight; this angle ranged from 10'-64' in 10 subjects, the average being 30.7'. Transfer to an unexposed eye was less than 1'. Opposite effects can be simultaneously induced in the two eyes at the same strength (given the same exposure time) as the binocularly induced effects (Shattuck and Held, 1975; Kavadellas and Held, 1977). Such opposite effects can be employed as a way of rendering the very small deviations from straightness visible, for, being opposite, they lead to the test field's seeming to be folded along its midline and inclined towards or away from the observer in the third (depth) dimension.

Held and Shattuck's last paragraph asks "are the channels demonstrated by our results the same as those responsible for the McCollough effect? We suspect so, but the definitive answer must come from parallels established by further investigation of both phenomena". The fruits of later researches by Held's group are summarised below. If they are compared with the corresponding data on the tilt aftereffect and the McCollough effect in table 2 it will be seen that whilst it resembles the McCollough effect in all but one respect (spatial frequency dependence), its sole resemblance to the tilt aftereffect is in the angle to the vertical at which the inducing gratings produce the largest aftereffect. (This angle is about 11° for the tilt effect, Gibson 1933; Campbell and Maffei, 1971).

Properties of Held and Shattuck's effect;

1.10.1 Growth. The effect continues growing with prolonged inducing periods for over an hour (Kavadellas and Held, 1977).

1.10.2 Time to Decay. Though Held and Shattuck 1971 report that 24 hours later the effect was not statistically significant, Held (personal communication, 1977) writes that "a 20 min inducing period will produce a discernible aftereffect for at least 24 hours later".

1.10.3 Monocularity. It does not transfer to an unexposed eye. (The otherwise extreme contrast between this aftereffect and the 100% transfer of the tilt effect is tempered by the fact that the tilt aftereffect loses colour specificity in transfer; Lovegrove and Over, 1973).

1.10.4 Angular dependencies. Held and Shattuck's effect peaks for inclinations of the inducing gratings of 11-15° to the zero position. No "indirect effect" is generated by inducing gratings approximately perpendicular to the test grating (Held and Shattuck, 1971). (For the tilt aftereffect the secondary maximum at the perpendicular orientation is of about half the strength of the principal one.) Held and Shattuck's effect is inducible at 45° to the vertical (Held, 1973) and is then only 12.5 % less strong than when induced near the vertical. This points to a site for the effect where azimuthal differences are small.

1.10.5 Spatial frequency dependence. Held and Shattuck's effect is strongest when test and inducing gratings match in spacing, and increases with increasing fineness of the gratings up to 16 cycles per degree (Held, 1973). (In this last respect it differs from both tilt aftereffect and McCollough effect.)

1.11 Spacing contingent upon colour

Alternate exposure to a wide red vertical grating and a narrow green one as described in section 1·6 simultaneously induces two aftereffects which are the inverse of each other. In addition to the chromatic a-e's visible on achromatic vertical gratings, there is an apparent difference in grating spacing, visible on a single vertical grating of intermediate spatial frequency, when its upper and lower halves are illuminated by red and by green light (Virsu and Haapasalo, 1973, and also Wyatt, 1974). The gratings used by Virsu and Haapasalo were of 7 and 2.5 cycles per degree for induction, and 4 cycles per degree for testing. After 15 min of inducing exposure, 7 out of 8 subjects reported that the density of the bars in the bipartite test appeared greater in the half field whose colour had, during induction, been paired with the wider grating spacing. As a function of the spatial frequencies used in induction and testing Haapasalo (1973) reports that the a-e strength "appeared to follow a course similar to that of the effect of Blakemore and Sutton". It should, however, be noted that the inducing situation differed from that of Blakemore and Sutton in that the whole region of the visual field to be exposed to the test gratings was exposed equally to both widths of coloured grating. As a function of inducing time the effect showed similarity with the McCollough effect, for it "became stronger when the adapting time was increased from 15 to 30 min."

Several contingent aftereffects involving moving patterns, both coloured and black and white, were discovered before the next two effects, but they are placed here to complete the section on stationary patterns.

1.12 A tilt aftereffect contingent upon spatial frequency and a spatial frequency shift contingent upon tilt

In 1974 Wyatt reported that after 30 min of alternate viewing, for 10-15 sec apiece, of a fine and a broad achromatic grating tilted respectively 15° clockwise and 15° anticlockwise from the vertical, the following two aftereffects were obtained*. Firstly a bipartite test figure, consisting of two vertical achromatic gratings, fine in the upper half field and broad below, appeared kneed to the right (to 5 out of 9 subjects). Secondly, a grating genuinely kneed to the left and of a single spacing throughout intermediate between those of the two inducing gratings, appeared (to 5 out of 8 subjects) kneed still, but more broadly spaced in its upper than in its lower half. The dependence of the above tilt aftereffect upon test spatial frequency was explored by Wyatt. After exposure to gratings of 3.2 and 6.4 cycles per degree, two subjects set to apparent vertical each of a set of 7 gratings covering the range 1.6-12.8 cycles per degree.

*This is Wyatt's experiment I. The fine grating was of 3.4-5.6 cycles/degree, the broad had double this spacing.

The tilts to either side of vertical were largest for gratings of the two spatial frequencies used during adaptation, the difference between the peak tilts being 1-3°.

Only below about 2 cycles per degree (and at the cross over point at about 4 cycles per degree) were their settings unaffected by the adaptation.

1.13 A "doubly contingent" aftereffect

Wyatt (1974) next proceeded* to induce two aftereffects in tandem. A 30 min exposure to a fine green vertical grating alternated with a broad red vertical one, induced the chromatic a-e contingent upon spacing (of section 1.6). This was followed by a 30 min exposure to tilted achromatic gratings as described in the previous section, 'fine' and 'broad' retaining the same values throughout both these exposures. When the kneed test grating of intermediate spatial frequency was then inspected, 4 of 8 subjects reported not only the spatial frequency illusion described in the preceding section, but also pale chromatic negative aftereffects appropriate to these illusory spacings.

Wyatt offers two alternative explanations of this doubly contingent effect. He admits that his experiments do not permit one to decide between them, but is himself attracted by the economy of supposing that tuning occurs along several dimensions of a single visual information channel. The second possibility is that the distorted output from one biassed system is fed as input to the next system.

1.14 Colour contingent upon motion

Although Norva Hepler (1968) credits both Celeste McCollough and Charles Stromeyer with having made unpublished observations which confirm her own, hers was the first published report of an effect in which the apparent hue of an achromatic patterned field changed when the direction

*This is Wyatt's experiment 3

of motion of the field was reversed.

1.14.1 <u>Induction and decay times</u>. Hepler's 8 naive subjects viewed horizontal stripes moving alternately up and down (for 5 sec apiece) by magenta and yellow-green light respectively in an otherwise dark room. That the aftereffect obtained under these conditions was not strong is evident from the fact that a minimum of 33 min and an average of 4 half hour sessions on successive days was needed before "they clearly saw a negative aftereffect specific to each direction of motion". Nevertheless, once induced it was long-lasting: a further 8 naive paid subjects were exposed for the half hour sessions but were not tested until 20-27 hours after each exposure. After an average of 8 inducing sessions and a minimum of 48 min, they too were reporting the chromatic aftereffects.

Stromeyer and Mansfield's (1970) 4 subjects by contrast "all saw the red and green colours" after only 20 min of induction. This may be the result of inter-subject differences which can be large (e.g. Favreau's 1976a table of results for 20 subjects in a related experiment) but the improvements in their apparatus over Hepler's are probably largely responsible for the more rapid results. Thus their use of two sets of stripes moving in opposite directions during both induction and testing, together with a fixation light will have reduced involuntary tracking by the eyes and will have rendered small hue differences more indubitably visible during testing. Moreover having the room illuminated instead of dark during testing, by providing an illuminated surround may have helped enhance this effect as it does the motion aftereffect (Strelow and Day, 1971). Stromeyer and Mansfield's stripes were moved at 4 degrees per second which was twice as fast as Hepler's and they further observed that if subjects were allowed to adjust "the speed... till the colours appeared most saturated", they chose speeds higher by 20% than those used during induction, and that at low speeds of "about 2 seconds per degree the colours vanished". These observations together with the fact that "the colours were most saturated" just after the test stimulus reversed direction and faded 2-6 sec thereafter, suggest that acceleration may be involved in this aftereffect.

A further experimental difference was in the frequency of reversal of direction during induction - every 5 sec (Hepler) every 10 sec (Stromeyer and Mansfield), but it has been shown (Favreau, Emerson and Corballis, 1972) that over the range 10-150 sec this factor makes no significant difference to the aftereffect strength.

Stromeyer and Mansfield note that immediately after the end of the exposure to the coloured belts the aftereffect colours are obscured by a simple chromatic aftereffect - both belts appearing grey for 30-70 sec. In section 1.15.1 a corresponding reduced sensitivity to motion is described following a similar exposure.

1.14.2 Monocularity

Using the striped belts Stromeyer and Mansfield found no transfer of the effect to an unexposed eye after a 20 min exposure in 4 subjects and were able in 30 min to produce opposite effects in the two eyes by exposing the eyes alternately for a minute apiece to oppositely paired moving coloured stripes.

1.14.3 Retinal specificity

Since the days of Helmholtz there have been suspicions that motion aftereffects might be the result of conditioned eye-movements. The control experiment of using a spiral (Plateau 1849) rules out linear eye movements. A spiral was used by Stromeyer and Mansfield to show both that linear eye movements were not responsible for the new chromatic aftereffect contingent upon motion and that it was "highly localized upon the retina". They illuminated the left and right halves of a spiral by red and green light resp. the two colours meeting in a sharp line through the centre. Each time the direction of rotation of the spiral reversed, the colours of the two half fields were also exchanged. After only 10 min of fixating the centre of the spiral 4 of the 5 subjects saw "the red and green after effects" in the two halves of the achromatic spiral when it was rotated. The colours switched halves at each change of the direction of rotation.

1.14.4 A rough measure of the angular tuning of this effect was obtained using the striped bands (Stromeyer and Mansfield, 1972) by asking subjects to tilt their heads sideways and to "locate the point at which the colours appeared one-half as saturated as when the head was upright and also the point at which the colours vanished". The mean results were 15 and 25° resp.

1.15 Motion Contingent upon colour

The report of a possible converse of the McCollough effect by Held and Shattuck (1971) was followed by the discovery of the converse of Hepler's colour-contingent-upon-motion effect. It was realised that an exposure, such as hers, to a pattern moving alternately in one direction in red light and the opposite way by green light, yields two aftereffects; firstly, as she reported, illusory hues seen only on moving achromatic test fields, and secondly (Favreau, Emerson and Corballis, 1972; Mayhew and Anstis, 1972) an illusion of movement seen on the stationary test field only when it was illuminated by reddish or greenish light. The aftereffect was again a negative one, the direction of the illusory motions being the reverse of those paired with the colours during induction of the effect. Both the above teams used spirals as stimuli; but whereas Favreau et al rotated their patterned disc at a high speed so that the spiral expanded or contracted at 1 degree per second, Mayhew and Anstis superimposed on their 4 throw spiral a network of fine black lines (letratone 102,a 'crazy paving' for draughtsmen) and rotated the disc at only 5 rpm because they found this arrangement gave "an extremely large simple rotary motion aftereffect" (though no radial motion).

1.15.1 Temporal properties. After 10 min of exposure to the inducing stimuli (with colour and direction of motion alternating every 10 sec), both teams found that the motion aftereffects were weak and were visible only briefly (usually for 1-2 sec) after each change in the colour of the stationary test spiral. Nevertheless, the aftereffect was long lasting: Favreau et al made a delayed test 24 hours after the first tests and found "virtually no decline" in the frequency of reports of motion by their subjects. This result is, of course, in remarkable contrast to the ordinary waterfall aftereffect which lasts 20 sec following a 2 min stimulation (Eysenck and Holland, 1960) and somewhat over 4 min after a 5 min stimulation (Taylor, 1963a).

The sensitivity to acceleration of the chromatic aftereffect contingent upon motion has already been remarked upon (1.14.1). Mayhew and Anstis (1972, p84) consider that rate-sensitivity is a general feature of the motion aftereffects contingent upon the various parameters which they studied.

Mayhew and Anstis found that the aftereffect was initially weak or zero but grew during the ½ hour after induction. Favreau, (1976a) who has replicated this result using discs with black patterning, finds that the initial weakness of the effect is absent if discs bearing coloured shapes devoid of luminance contrast are used. With discs bearing orange+red and blue+green patterns she reports that the colour contingent aftereffects start strong and decline with time. She suggests that the black patterning, which had been presented to the subject moving in both directions during induction, had an inhibitory effect which took about ½ an hour to wear off. This superimposed motion effect seems to be a parallel to the overlying chromatic effect observed when testing for the motion contingent chromatic effect produced by the same exposure to coloured moving stimuli (section 1.14.1).

1.15.2 A conditioned response? Mayhew and Anstis noted that much testing reduced the effect to zero, but that after a ½ min rest the aftereffect recovered and "could still be elicited hours and even days after adaptation". Their feeling that these temporal characteristics of the effect resembled those of "perceptual learning" and of conditioning rather than those of physiological adaptation of "double duty" units led them to make two further experiments - the first on 'extinction' and the second on 'transposition'. They found that the colour contingent motion aftereffect was "remarkably resistant to extinction"; 15 minutes of exposure to alternating unpatterned red and green fields and 5 min to achromatic moving fields served only to reduce but not to extinguish the aftereffect which was then "restored by a 2-min rest in the dark and was reported by two of the 4 subjects as still present, though very small, 2 days later".

In the experiment to test for transposition they explored whether the same colour could, in a different context, elicit opposite impressions as to the direction of motion of the stationary spiral. Following a 10 min exposure to, for example, yellow counterclockwise and red clockwise viewed alternately, testing was by a series of coloured illuminations such as red-yellow-green-yellow (Wratten filters 25,12,58 resp) presented for 5 sec apiece. The subjects' response series was counterclockwise-clockwise-clockwise-counterclockwise, i.e. the response to the yellow spiral depended upon which colour had immediately preceded it. This is describable of course as transposition, and a single cell would not normally be thought of as giving such results. Nevertheless one may ask whether it is possible to explain these results in peripheral terms without invoking anything so sophisticated as a mechanism capable of extracting invariants. The colour receptor system which feeds the single cell may suffer temporary biassing of its sensitivity by each colour in the test sequence (cf von Kries 1905). If so the population of cones which respond most vigorously to the yellow light will be different according as red or green cones have been more strongly affected by the preceding light. Lengthening the interval between presentation of the colours should be instructive here. Testing with the coloured areas side by side simultaneously might also provide an informative control.

Similar transposition tests have been devised by Mayhew and Anstis (1972) for two other motion aftereffects (those contingent upon grating spacing and luminance), and in each case it is possible to point to non-central factors which could bring about the transposed results. This is not to dismiss transposition but to suggest that it does not of necessity imply a central locus for these aftereffects.

1.15.3 Monocularity of the colour-contingent motion aftereffect. No transfer of the colour contingent motion aftereffect to an unexposed eye following a 10 min exposure was found by Mayhew and Anstis (1972) in 8 subjects or Murch in 6 (1974b). Mayhew and Anstis were able to produce opposite effects simultaneously in the two eyes, and Murch in the two (left and right) halves of one retina by exposing first one and then the other to oppositely paired stimuli. In these latter respects the colour contingent aftereffect does not differ from the ordinary motion aftereffect (Gates, 1934; Walls, 1953), but the complete lack of transfer to an unexposed eye is at first sight remarkable since the ordinary motion aftereffect transfers strongly (Dvořák, 1870; Holland, 1957) in a sizeable proportion (9/25) of subjects (Pickersgill and Jeeves, 1958). It has however, been reported that such chromatic selectivity as the ordinary motion aftereffect possesses monocularly is lost in transfer (Lovegrove, Over and Broerse, 1972; Day, R.H. 1977), so the above lack of transfer of the colour contingent aftereffect may be seen as a related phenomenon.

Nevertheless the colour-contingent motion aftereffect is not entirely monocular. Murch (1974b) has claimed that a 5 min dichoptic exposure of the left eye to magenta and green unpatterned fields while the right eye fixated the centre of a spiral which rotated alternately clockwise and anticlockwise led to consistent motion effects in the appropriate directions" being seen with the left eye by 5 out of 8 subjects on the stationary spiral when it was lit alternately by red and green light. Murch sees this as pointing to an "association between monocular color detectors and binocular motion detectors".

1.15.4 Motion contingent upon the colour of a surround

A variant of this motion effect in which the colours were restricted to an area immediately surrounding an achromatic spiral also produced a negative motion aftereffect (Potts and Harris, 1975). Controls in which the stationary spiral as well as the surround were illuminated by coloured light ruled out the possibility that this effect was ascribable either to simple aftereffect colours imposed on the spiral by eye movements or to simultaneous contrast colours.

1.16 Achromatic Motion-aftereffects

In 1969 a startling contribution to the already large and venerable literature on the ordinary aftereffect of seen motion encouraged the search for motion aftereffects contingent on parameters of the test situation other than colour. As has been already mentioned (in section 1.15.1), the duration of the ordinary waterfall effect is of the order of 8 sec - 4 min.

Masland (1969), however, reported that more than 100 subjects still saw a negative movement aftereffect 24 hours after a 15 min exposure to a rotating black and white spiral if, and only if, they viewed the now stationary spiral. Unless they fixated within 1.5° of the central point which they had fixated during induction of the effect, they saw no movement of the 5° spiral or of anything else. "But when", Masland says, "the eyes return to the fixation point the spiral suddenly begins to move; the motion can be started and stopped merely by shifting one's line of regard by a few degrees". More than 14 naive subjects were kept in the dark for 10 min after the inducing exposure and were not shown the stationary spiral until 24 hours later. They then all reported seeing movement in the negative direction.

Masland obtained a graph of the time course of decay of this pattern contingent motion aftereffect by asking subjects during testing so to control the spiral's actual speed of rotation that it appeared to them to be stationary. Each of 72 subjects was tested at one of 5 possible times after the end of induction. The resulting average graph falls to ¾ of its initial value within the first 15 min but thereafter falls very gradually to 2/3 after 24 hours.

The realisation that there are two ingredients in the movement aftereffect - a pattern-contingent one as well as the non-contingent part which can be seen even with closed eyes - clarifies the diverse reports as to the influence of 'well-marked' patterning of the test field on the duration and 'vividness' of the aftereffect (cf Mach, 1875, Budde, 1884 and Wohlgemuth, on pp.7, 12, 35 of Wohlgemuth 1911, also Holland 1965 p.9.). The contingency upon pattern was in fact implicit in the mode of testing each half retina used by Walls (1953). The next step was to isolate those parameters of the achromatic test pattern upon which, in such an experiment as Masland's, the motion aftereffect was contingent.

In the following few years several parameters were explored and at least three corresponding motion aftereffects discovered - contingent upon the texture density, polarity of contrast and some aspect of the luminance of achromatic patterns.

1.17 A motion aftereffect contingent upon texture

In 1972 Walker* reported a visual motion aftereffect contingent upon visual texture density: two white circular discs each bore the same random pattern of at least 100 black dots but with a difference in magnification of 6.3:1. The discs were set side by side or (in a later design which eliminated eye movements) were viewed alternately in a two-way mirror against a black background. They rotated in opposite directions at 8 rpm and were alternately illuminated for 4 secs apiece, the subject

*Footnote

In 1966 Walker had reported a suggestive simultaneous-contrast effect in another modality: after the fingers of the two hands had been stroking two different grades of sandpaper - coarse and fine - a medium texture touched by both hands seemed coarser to the hand which had previously been touching the fine paper, than to the other hand.

fixating the centre of whichever was visible. A 4 min exposure period was followed by 1 min in the dark and then the subject was shown both stationary discs and "was asked to fixate the centre of each disc and to indicate the direction of apparent rotation". Of the 16 subjects, 8 saw movement of both patterns in the direction opposite to that which it had had during induction of the effect. The average result for the remaining eight was in this direction also but less clearly so. A similar effect induced by "medium" and "narrow" (2 and 4 cycles per degree resp) horizontal gratings moving up and down resp in two adjacent panels and switched in spacing and direction every 10 sec has been reported by Mayhew and Anstis (1972). Of 12 subjects 10 saw motion aftereffects on stationary "medium" and "narrow" gratings after 10 min; 5 'transposed' effects on "wide" (1 and 2 cycles per degree) and "medium" test gratings. Since these were presented side by side and exchanged positions every 5 sec, it can be expected that simultaneous and sequential contrast in the spatial frequency domain (MacKay 1973 and Blakemore and Sutton, 1969 resp) will have influenced the perceived spacing of the gratings, the medium seeming narrower than it is. If so, this experiment on 'transposition' may be seen as a demonstration that spatial frequency distortions occur prior to the texture contingent motion aftereffect.

1.18 <u>Motion contingent upon luminance</u>

Mayhew and Anstis (1972) reported a further pair of aftereffects visible on the achromatic patterned spiral described in section 1.15. The first they describe as a motion aftereffect contingent upon its brightness; the second, its inverse, is an apparent brightness difference which depends upon the sense of rotation of the disc. Two inducing conditions and their corresponding test situations were employed. In the first condition the luminance of the whole disc alternately took two values separated by 1.5 log units and these were paired with the disc's alternate clockwise and anticlockwise rotations. In the second the upper and lower halves of the disc were simultaneously given opposite pairings of luminance and sense of rotation; for example, a bright upper half and dimmer lower half were paired with clockwise rotation, and alternated every 10 sec with dimmer upper half/bright lower half and anticlockwise rotation.

After 10 min the motion aftereffects seen on the stationary disc under various luminance conditions were reported; while the results lead one to keep open the possibility that there may be a motion aftereffect contingent upon luminance, they do not compel this conclusion. The most striking feature is that the brighter stimuli induced,and evoked in testing, stronger effects than the dimmer ones. Throughout the results the authors remark on assymetries which point to this, and which raise the possibility that the results are simply attributable to ordinary motion effects whose strength is greater for more luminous inducing and test fields (Wohlgemuth, 1911). The negative motion aftereffect corresponding to the brighter (or brightening) test field was reported by all but one of 14 subjects while the direction of motion corresponding to the dimmer condition was always weaker and often zero. Under the 'whole field' conditions of inducing and testing, motion was reported at the dimmer illumination level in only 3 out of 12 tests on 6 subjects and was "very small" and short lived. Under the split field conditions "the asymmetry was less marked but the subjects consistently reported that the brighter of the two half fields gave the larger CMAE". A doubt, however, lingers as to whether the well known power of the visual system to generalise may have operated here, for there was a clear aftereffect in the same rotary sense present on the brighter half field. Control tests in which each inducing condition (whole or split field) was followed by the other test condition would therefore have proved interesting. In each case apparent rotation in opposite directions in upper and lower half fields would be expected if the aftereffects are truly contingent. In summary, though the evidence for a motion effect contingent upon absolute luminance is not strong there may at least be a motion effect contingent upon the relative luminance of two test areas.

1.18.1 The overriding aftereffect in response to the brighter field casts doubt also on the transposed results. Without artificial pupils, pupil adjustment will have somewhat reduced the (0.6 log units) luminance differences applied, so it is not surprising that transposition occurred much more often with the split field, than with the whole field at a single luminance. This suggests that the relative luminance of the two halves was important, but whether as an ingredient in induction or testing cannot be said.

1.18.2 It may be noted in passing that there have been differing reports as to whether the ordinary aftereffect of motion is sensitive to the luminance and contrast of the inducing and test figures (Wohlgemuth, 1911; Day, 1957; Over and Broerse, 1973). The most opposite study is that of Over and Broerse which suggests that over the range 1-45 cd/m^2 distinctly larger effects (by 13-50%) were obtained when the space average luminance of the test stimulus was the same as that of the inducing stimulus.

1.18.3 Luminance contingent upon motion. The inverse effect, of an illusory luminance difference seen on the upper and lower halves of the rotating disc, does not demand explanation in terms of a contingent aftereffect. It may show only that greater 'fatigue' was produced by the brighter motion stimulus.

1.18.4 Mayhew and Anstis conclude this section on luminance effects by describing a "brightness analogue" of McCollough's effect. The 40 min which this takes to fade following a 20 min induction (V. MacKay, unpublished observation) corresponds so well to the time which grating contrast threshold takes to recover from exposure to a single achromatic grating (Heggelund and Hohmann, 1976) that there seems here insufficient evidence to date for regarding dim as different from bright in some sense other than magnitude.

1.19 Polarity of contrast as a variable which influences the duration of the ordinary aftereffect of motion.

After fixating for 5 min the centre of a slowly rotating pattern which was alternately, for 3 sec apiece, a black and white crazy paving pattern or its photographic negative (moving clockwise and counterclockwise respectively), the durations of the simple motion aftereffects produced by 13 sec exposures to similar patterns were measured (Mayhew, 1973). In these tests each pattern was moved in the same and the opposite direction to those employed during the prior exposure. It was found that the motion aftereffect thus generated lasted a significantly shorter (average 1½ sec) time when the patterns moved in the same direction as previously than when they moved in the opposite direction. (Control experiments were performed for the possibility that it was the "space average luminance" that was responsible). When the test patterns differed in scale by a factor of two from the inducing patterns, although the aftereffects lasted slightly longer, the difference between their durations was only very slightly reduced.

Mayhew remarks that since "a motion system that was sensitive to spatial frequency could not distinguish between the adapting patterns used", this experiment shows that phase or the polarity of contrast of the pattern must be involved in the motion aftereffect and he makes reference to the brightness and darkness channels of Jung (1971). Although I think he is right in seeing contrast as the important variable (see Appendix II) his experiments do not, in fact, control for the possibility that not polarity but the average size of either the black or the white pattern elements was the factor upon which his results were contingent (cf Walker, 1972 and Uhlarik and Osgood, 1974). His finding that doubling the pattern scale exerts only a small influence on the aftereffect duration would be seen as hardly surprising because the black "paving stones" of the pattern are some ten times as wide as the black "cracks" of the photographic negative. Appendix II describes the pattern-contingent aftereffect which corresponds to Mayhew's observations, and uses a form of patterning which makes it more clear that the aftereffect is indeed contingent upon the polarity of contrast of both dark and light enclosed shapes.

1.20 A motion aftereffect contingent upon binocular disparity

If the pair of shadows cast by two horizontally adjacent sources of plane polarised light are binocularly viewed through suitably oriented polaroid filters, the identical pattern can be seen with either crossed or uncrossed disparity depending on the pairing of the polaroid filters at the eyes and at the sources (Gregory, 1964). By this means a randomly patterned disc was binocularly presented with disparities of 0.1 degree rotating (at 4 rpm) alternately clockwise and anticlockwise in planes apparently in front of and beyond the fixation point for 10 sec apiece

(Anstis and Harris, 1974). After 30 min of exposure to this stimulus a pair of contingent aftereffects were obtained: the stationary disc appeared to rotate anticlockwise or clockwise according as it was presented in front of or behind the fixation point, and conversely the test field, when presented in the plane of fixation, appeared to be a few millimeters farther away when rotating clockwise than when rotating anticlockwise. The first effect was strong - stronger than the motion effect contingent upon colour when pitted against it - and lasted nearly 30 sec upon the first inspection. Its duration upon successive test inspections fell exponentially to near zero in 5-37 min. The second effect was "extremely weak and disappeared within a minute or two after adaptation".

1.21 Colour and Binocular disparity. It has been reported that using Julesz patterns a stereo depth analogue of the McCollough effect was not obtained after 40 min induction (Over, Long and Lovegrove, 1973). The analogy was not strictly complete for the 2 stimuli (red/uncrossed disparity and green/crossed disparity) do not appear to have been presented in one and the same region of the visual field. Stromeyer, Dawson and Brown, (1976) have also failed to obtain a colour and depth effect.

1.22 Aftereffects contingent upon direction of gaze.

1.22.1 Prof. T. Erisman and his student Ivo Kohler noticed that during the first three days of wearing prisms before the eyes there was a marked decrease in two geometrical distortions produced by the prisms, and also that corresponding negative aftereffects were seen when the prisms were removed (Kohler, 1951). Since these two distortions alter very noticeably in strength as one turns or bows the head while fixating an object, the adaptation to them has a considerable gaze - contingent ingredient. The two distortions are the stretching and compression perpendicular to the prism edge (i.e. horizontally in Kohler's case) and the scissors-like flexing of angles. The adaptations to these two effects are possibly distinct from each other, for the adaptation to shearing eventually cancels the real angular flexings (produced by head nodding) more completely than does that to stretching and also reaches its saturation value more rapidly (Hay and Pick, 1966). These two adaptations and their aftereffects presumably point to a modification of the average mapping of space in the right and left and upper and lower parts of the visual field. That the modifications are tailored to the position of the eyes in their sockets suggests that signals from the ocular motor system are involved in this contingent effect. If so the field to be encompassed by thinking about contingent aftereffects is considerably widened.

1.22.2 Kohler (1951 and 1962) has claimed that two-coloured goggles with a vertically divided field, e.g. yellow to the left and blue to the right produced gaze - contingent chromatic effects. These effects were as delicate as the difference between two shades of note paper - with gaze left a white paper appeared a "slightly soiled white" and with gaze right had a "faint bluish tinge" (McCollough, 1965a). Kohler's test conditions (McCollough, 1965a) consisted of a 12° near-white rectangle of adjustable colour within a 40° dark surround, beyond which lay the illuminated room.

McCollough (1965a) wishing to make foveal CIE measurements of this effect wore red/green filters on the right eye for 75 days but her careful comparisons of the left with the right eye then revealed no significant gaze - contingent hue difference in the exposed (L) eye. (Two 2° test areas were each seen by one eye alternately in a completely dark field and the hue of the left eye's patch could be matched by the subject to the right eye's "daylight".) Under ordinary viewing conditions also she saw no gaze - contingent hue change on a white wall. Harrington (1965) using red/green filters, provided by Kohler for both eyes, likewise observed no gaze-contingent effect. Leppmann and Wieland (1966) on the other hand, using yellow and dark blue spectacles with a large (x4) difference in attenuation between the two filters, report a replication of Kohler's chromatic findings and also a large brightness difference across the visual field. Their report, however, is anecdotal and only brief mention, with no systematic testing, is devoted to the alteration of hue of a "movie screen" when the head was turned through 45°.

McCollough (1965a) regards the effects observed by Kohler as a consequence of the gradation of yellow to blue adaptation across the retina. As the eyes are turned in the head she suggests (p374) that simultaneous colour contrast with that part of the periphery which is not viewing the inside of the nose or cheek slightly modifies the hue perceived foveally. In support she draws attention to the apparent yellowing of a grey field when a small blue spot of light is placed in the visual periphery.

Mayhew (1973b) has reported a movement aftereffect contingent upon direction of gaze. By turning the eyes to and fro horizontally through 20°, 6 subjects viewed alternately two counter rotating but otherwise identical patterns. After only 3 min of exposure they all reported seeing negative aftereffects on whichever (stationary) pattern they viewed. Mayhew suggests that the results may be attributed not so much to "double duty" units as to "some form of active adaptive response to the invariances in the adaptation procedure". The possibility (since the aftereffect is only small (p878)) that a learned cyclotorsion accompanies the horizontal eye movement has been considered by Mayhew. He found that when the subject kept the eye at a given direction of gaze instead of bringing it there by a sideways motion, although his subjects' reports of motion in the appropriate direction were reduced, they were not abolished. To further clarify the factors upon which this motion after effect is contingent it might have been interesting to bring the eye in to the target direction of gaze from both sides and also from above or below.

1.23 Summary: contingent visual aftereffects

Over a dozen visual aftereffects have been described, each of which involves two parameters of the visual world. During the inducing exposure these parameters are so paired together that afterwards the real value taken by one determines the illusory value taken by the other. The visual parameters concerned are polarity of contrast, colour, pattern spacing, orientation, direction of motion, binocular disparity and possibly luminance. About half of the pair combinations of these parameters have been shown (1977) to generate aftereffects.

These aftereffects are all negative. None of them shows interocular transfer. They become stronger when the inducing exposure is extended to half an hour or more. They are remarkable for their durations which range from 2 minutes to over 24 hours.

The three explanations of these effects which had been offered up to 1972 were in terms of (a) the on-going 'normalisation' of the system on the basis of the average input from the environment; (b) selective fatigue of cells in the visual pathway which respond to two or more features of the visual environment, and (c) associative learning.

CHAPTER 2 FURTHER PROPERTIES OF THE MCCOLLOUGH EFFECT

Some of the principal properties of the McCollough effect have already been mentioned in the previous chapter (in sections 1.5 to 1.8). Further and more detailed literature on the effect is reviewed in this chapter. Some variables of the exposure situation are dealt with in sections 2.1 to 2.3, 2.4.6 and 2.7.12. The remainder of the chapter describes properties of the aftereffect.

The section on the growth of the aftereffect (section 2.1) and that on the attendant reductions in the visibility of gratings (section 2.5) have a bearing on the mechanism of the McCollough effect. The remainder are instructive as regards its possible locus.

Three topics are omitted from this chapter because they will be dealt with later in this thesis. They are the time course of decay of the McCollough aftereffect, binocular involvement in the effect and the resemblance of the conditioned aftereffects to conditioned responses. The literature on these subjects will be considered in chapters 5, 6 and 9 resp.

A summary of the most significant properties of the McCollough effect appears in chapter 9.

2.1 Growth of the McCollough Aftereffect during Induction

2.1.1 Saturation of the McCollough aftereffect hues

The saturations of both the green and the red hues seen as aftereffects upon achromatic gratings increase most quickly during the first few minutes of exposure to two alternately presented, differently coloured, orthogonal gratings (a McCollough exposure). The saturations of both hues grow by at least a quarter (Hajos, 1969) and in the absence of testing by nearer a half (Riggs, White and Eimas, 1974) with each successive doubling of the exposure duration from 2 min up to 16 min. The hues still continue gaining strength when the McCollough exposure is prolonged beyond 25 min (Riggs et al, 1974), approaching a ceiling after 1½ hours (Stromeyer 1971).

After 5-10 min of McCollough exposure the hues seen on achromatic gratings at ordinary photopic levels of illumination are rather pale. For example, following a 7 min McCollough exposure (to orange and blue-green gratings, Wratten 16, 47 resp. at 10fc) the average saturations of both the green and the pink aftereffects for 21 subjects who made tristimulus colour matches to the two orthogonally striped areas of an achromatic 10fc test field were only 10% and 11% resp. (Hirsch and Murch, 1972). There were, in addition, 7 further subjects who, though "colour normal" and "competent" in making colorimeter matches to real colours, registered and verbally reported no coloured aftereffects. Results of only 3-4% saturation were obtained for six subjects on 5.2ftL test fields (Riggs et al, 1974) following a similar 10 min exposure to magenta and green gratings (Wratten 34A, 53 resp at 5.2ftL). The latter measurements were made using a cancellation technique in which the subject was asked to add coloured light to each of the two orthogonally striped areas of the test field in such a way as to keep them matched in hue. The strongest aftereffects that have been reported are 55% and 40% for the red and green resp. These colorimeter readings were made (with one eye while the other viewed the achromatic grating at 1.65ftcd), 30 min after the end of a 90 min exposure to green (530nm) and red (620nm) alternated gratings. (Timney, Gentry, Skowbo and Morant, 1974). If the test field is very dimly lit in the mesopic range the hues look stronger. After nearly two hours of exposure to green and red gratings (Wratten 55 and 26 resp). The Munsell chips (at 4.6ml) which were selected, using the left eye, as colour matches to achromatic gratings at 0.085ml, viewed by the right eye included 5R 6/8, and 5G 8/4 after 30 min and 5R 7/8, and 7.5G 6/6 (Stromeyer, 1971).

2.1.2 Measurement of the Growth of the McCollough effect

There are two possible ways of measuring the increase in McCollough aftereffect strength as a function of exposure duration, each of which has a merit.

Hajos (1969) interrupted the McCollough exposure at intervals to make measurements of the aftereffect strength. This method has the merit that the subject is in a similar metabolic state throughout, so the scatter of results is only moderate. It has the drawback, of course, that rapid decay occurs during each test period (cf Chapter 5), so the resulting plot of the growth of the aftereffect cannot but fall somewhat below the values which the aftereffect would have been attained in the absence of testing.

Riggs, White and Eimas (1974) employed the alternative and more satisfactory method of exposing the same subjects for different uninterrupted lengths of time on several separate occasions and measuring the aftereffect at the end of each exposure.

(The colour mixers used in the above measurements are described in the supplement to this Chapter 2.8.4.4-5)

Both methods yielded a similar form of curve with a rapid increase in the first four minutes and only about a third as much growth in the next four minutes. The results yield straighter lines when plotted on log/log coordinates than on the semi-logarithmic coordinates chosen by Riggs et al (1974) for their Fig. 3. Over the range 1-10 min the average slopes of the log/log plots range from 0.31-0.44 (Hajos, 1969) to 0.55-0.7 (Riggs et al, 1974). That the nett growth is so much smaller in Hajos's experiment is probably attributable to the high luminance (6ml) and considerable durations of the testing in which "a short break" was followed by eight colour matchings.

Hajos (1967) also studied the manner in which the aftereffect strength (as judged from the percentage of 'correct' replies) returned to zero when the regular cycle of exposure and measurement that had been used to induce an effect was continued but with the inducing stimuli turned through 90°. The curve for cancellation of the effect was close to the inverse of the growth curve, the effect being removed slightly faster than it had been induced.

2.1.3 The time scale of this growth process is much more protracted than that of any other purely visual aftereffect (apart from the other contingent aftereffects). Only those effects which involve eye-hand coordination and non-passive locomotion and movement have comparable time constants (cf Table 2). The figural aftereffects, the Gibson bent line illusion, the spatial frequency shift and ordinary chromatic aftereffects all attain saturation within less than 5 minutes of exposure to appropriate stimuli. There is, of course, the possibility that the stimuli generally employed to induce contingent aftereffects are grossly inefficient. But all attempts so far to induce effects more rapidly by suitable selection of obvious variables such as the luminous intensity, colour, spatial frequency and presentation rate of the two gratings have yielded only minor improvements. (2.9.2)

The high saturations eventually obtained indicate that a considerable fraction of the visual input is passing through the McCollough-biassed system.

2.2. Timing of the Stimulus Cycle

Hajos (1969) altered the duration of the individual presentations of the two coloured gratings and the length of a dark interval between them and the total duration of the exposure. His most intriguing discovery was that the aftereffect strength depended upon the total induction time, including dark periods.

For example, when 10 min of grating presentation was spread out over 30 min by changing the stimulus cycle from 1 sec 'on'/zero sec 'off' to 1 sec 'on'/2 sec 'off', the aftereffect was doubled in strength. This is the very same growth rate - a doubling of the aftereffect for a tripling of the induction time - which was later found by Riggs et al in the uninterrupted exposures with no dark periods (mentioned above). This finding suggests either that a process of consolidation takes place in the dark intervals, or that diminishing returns set in when the light is on for a large fraction of the cycle, or both.

2.2.1 Hajos (1969) then compared the aftereffect strengths obtained using a single stimulus rhythm and varying the cycle length over the eightfold range from ½ sec 'on'/½ sec 'off' upwards but found no significant trends. White and Ellis (1976, and White, 1976) have since extended the range greatly (but using no dark intervals) and found that with 'on' times of below ½ sec the aftereffect decreases to about one third of the maximum value which it has for grating presentations in the range 50 - 1 sec.

2.2.2 A further study of the timing of the induction cycle, in which pattern and colour were presented separately with a variable intervening dark interval is described in a later section (2.4.3) (Murch and Hirsch, 1972) and also Chapter 9.2.5 (Murch, 1976).

2.3 Alteration of the position of the stimulus on retina during induction

2.3.1 Fixation is not necessary during induction or testing (McCollough, 1965b). Harris and Gibson (1968a) tried to eliminate the possibility that the McCollough effect was nothing more than simple afterimages acquired by involuntarily fixating the same part of the grating upon each presentation. They presented the gratings as very brief (80 msec) flashes, with their positions on the screen systematically shifted by a half cycle, and still obtained a good aftereffect.

2.3.2 The converse possibility - that movement of the image over the retina was an essential factor in inducing an aftereffect - was advanced by Piggins and Leppman (1973) after finding that exposures to stabilised gratings produced no McCollough effect. Stromeyer and Dawson (1974), however, showed that aftereffects could be induced using a succession of flashes so short (60 microsec) that no appreciable eye movement could occur during each presentation, but sufficiently bright (10^6cd) that the afterimage was visible for 1-2 sec after each flash.

It seems, therefore, that neither fixation, nor motion of the inducing stimulus is essential for the production of McCollough aftereffects, but that the mechanism which produces fading of stabilised images precedes the site of the McCollough modification.

2.4 The Hues of the McCollough aftereffect and of the phantom fringes

2.4.1 The hues of the McCollough aftereffects as a clue to the mechanisms underlying the effect

The hues of the McCollough effects seen after exposure to various colours of grating are potential clues as to the way in which the four retinal receptor systems feed into the McCollough mechanism.

For instance, it was said by one of the two experimenters who have published most on the aftereffects produced by gratings of colours other than red and green, that the (McCollough) "aftereffects are basically red and green" (Stromeyer, 1969, see section 2.4.4). And the other (Hajos, 1970, see section 2.4.5) found that "not a single blue naming response (but 50% red and 40% green)" was produced by viewing a yellow inducing grating in combination with gratings of other colours.

Stromeyer later (1972, section 2.4.4) revised his opinion, but these earlier statements, had they held up for long (as well as for short) exposures might have been taken as showing that only the red and green cones feed into the McCollough mechanism.

Again, Hajos (1970, 1973) later claimed (see Section 2.4.7) that "the long wavelength yellow to red patterns produce a pink aftereffect which is at right angles to the orientation of the... (inducing) pattern". This claim, if substantiated, would have radically affected the picture of the connections which precede or form part of the McCollough mechanism - revealing perhaps, as Hajos proposed, "an opponent orthogonal inhibition". In the light of subsequent experiments both these early conclusions seem to be mistaken, but they are mentioned here firstly to illustrate the interesting type of pointers which may be gained from experimental evidence in this region, and secondly to provide a context for experiments which were later performed (chapter 8.1).

2.4.2 Hues of the Phantom fringes

In view of the later impression that the McCollough "aftereffects are basically red and green" (Stromeyer, 1969), it is interesting to turn back briefly to the phantom fringe literature and note that all experimenters describe as "blue", and rarely as green, the hue seen on that contrast edge which, during prism wearing had been bordered by a vivid red band shading to an orange-yellow zone. Thus Gibson (1933) after 4 days speaks of "blue" and "red"; Hay, Pick and Rosser (1963), after 10 days, of the "bluish" and "reddish" fringes seen in ordinary, and also monochromatic (642nm), illumination, Hajos and Hajos (1965) speak of "blue-green" and "orange". Kohler on his 12th day of prism wearing describes "bluish-violet" and "reddish-yellow" borders and on his 50th "bluish" and "yellowish" ones. After only 2 hours induction the present author described the pale colours seen as "turquoise" and "pink". In the phantom fringe aftereffect it therefore seems probable that all three cone inputs are involved.

2.4.2.1 Half-Spectra?

In passing, a disturbing phrase of Kohler's (1951, p26) may be noticed but not given undue weight; he refers to the aftereffect fringes as "half-spectra", saying "it was as if the subject had developed the power to break white light into its components". This description seems to have been called forth, however, not so much by the detailed appearance of the fringes as by their impressive ability to render completely invisible - by "exactly compensating for" - the real refractive fringes produced by the prisms. For example, when at a black and white movie (50th day) Kohler's real prism fringes "were not the tiniest bit visible" when wearing the prisms, though on removal of the goggles all non-horizontal edges had "distinct bright yellowish" or "bluish" edges - "nothing else", he exclaims, "but the exact negative offprint (Abklatsch) of the prism effects of the first days and weeks of the experiment". If this means that different hues were visible at different angular distances from the contrast edge, the mechanism of the prism adaptation is an order more complex than has been appreciated!

2.4.3 Hues of the McCollough aftereffects: Colour complements of the inducing colours?

McCollough (1965b) described the hues produced by alternately presented blue and orange gratings (Corning 2-73 and 5-56) as "blue-green" and "orange". McCollough and Clark (1970 unpublished and mentioned by Hirsch and Murch 1972) wondered whether the aftereffect hues are always colour complements of the inducing colours. They found, however, that changing the colour of only one of their inducing gratings altered the hues seen on both orientations of grating in the test figure. The evidence considered in section 2.4.3 suggests that this is probably a consequence of the changes in retinal colour sensitivity brought about by exposure to the preceding colour; that in section 2.4.4 suggests that if one exposure grating only is used the McCollough hues are colour complements of the grating colour.

2.4.4 The Hues seen after viewing a single coloured grating

To avoid complications introduced by changes in retinal sensitivity (2.4.3), it is desirable to expose the subject to only one coloured grating (e.g. Stromeyer, 1969; 1972b), on occasions sufficiently well separated to allow the effects of earlier exposures to fade completely. (Stromeyer did not in fact usually give the earlier aftereffects long to fade but 'neutralised' them by a fresh exposure to the same grating turned through 90°.)

Stromeyer's three subjects (1969 table 3) were exposed for 10 min to a single vertical grating, illuminated by one of a set of 18 narrow-band filters spanning the range from 404-620nm. When "several minutes" had been allowed for the non-contingent "afterimages to fade", the subject was shown an achromatic test field having areas of both vertical and horizontal stripes and asked to describe the hues they saw on each area and to allocate arbitrary subjective ratings to the saturations of these hues. The verbal reports included a wide variety of colours from "pinkish-purple" through "gold-yellow" and "yellow-green" to "bluish-green" and "greenish-blue" but conspicuously did not report blue or bluish violet. Also their saturation ratings were large only for the hues "red", "pink", "green" and various "yellows", the bluish and purplish hues being always feeble. As the wavelength of the inducing filter was decreased (starting from the red end of the range), the reported hues "showed a sharp reversal" from green to pink when the filter was in the region of "pure yellow" (582nm) and made a return to green in two of the subjects, and "gold" (rather than "pink") reds in the third, when tbe filter was near "pure blue" (476nm). The only reports of "no colour" in the aftereffect occurred at or near these reversals. It was these results that led Stromeyer to conclude that "the aftereffect on the vertical grating is clearly not the mixture complement of the adaptation grating" and that the "aftereffects are basically red and green".

Three years later, however, experiments using 30 min in place of 10 min inducing periods led him to revise this opinion - "it now appears that blue and orange-yellow aftereffects may also be obtained, although they are not as readily produced as the red and green effects" (Stromeyer, 1972b). He then describes the aftereffect hues as "approximately complementary to the adaptation colours". His measurements of the saturations of these hues (made on an adjacent unpatterned area whose colour purity was determined by polarizers in front of two projectors) show that the blue aftereffect was less saturated than the red green and orange hues by a factor of five.

While there seems, therefore, to be no reason to think that all three cone types do not feed into McCollough mechanisms, the blue aftereffect requires longer inducing times before revealing itself. This conclusion appears to be supported by the observations on the phantom fringe hues described above.

For evidence that the rods also affect the McCollough mechanism see

2.4.8: The McCollough effect visible at scotopic luminance levels.

2.4.5 The blue aftereffect is of weak saturation after brief exposures

The poor visibility of the blue aftereffect is further emphasised by an experiment in which more than one inducing grating was used (Hajos, 1967 expt IV). Eight subjects were given McCollough-style exposures for the minimum time necessary to elicit in six consecutive tests the same verbal report of the hues seen. (Testing, on a field bearing both orientations of grating, interrupted the presentation of the coloured gratings every ½ min) In the course of a series of runs the (horizontal and vertical) inducing gratings were projected through all possible pair combinations of a red, a yellow, a green and a violet filter (Wratten broadband with dominant wavelengths 660nm 580nm 520nm, 470nm). Hajos expected that if the hues of the aftereffects were complementary to those of the four filters, then 25% of all the hue namings should fall to each of the four possible colours; in fact the results were red:45%, green:28%, yellow:13%, blue:5% and 9% "no colour".

Hajos links these proportions with the highly similar ratios of on-centre red, green and blue cells then newly reported in the monkey LGN by Wiesel and Hubel (1966). But it would have been interesting to see whether the proportions remained unaltered given a longer exposure to the inducing stimuli. With stronger aftereffects a drift towards blue might be expected from the findings of Wilson and Brocklebank (1955), that real hues which at high saturations are perceived as blues, at low saturation look increasingly violet. It would also have been interesting if Hajos (and Stromeyer too) had obtained verbal hue judgements from their subjects of the ordinary chromatic aftereffects seen on the identical test fields after exposures of similar duration to those of their McCollough exposures. This would have answered the question as to whether blue aftereffects were difficult to see under the conditions used irrespective of the McCollough effect.

In summary, red and green aftereffects are much more readily noticed by subjects than blue and yellow ones but blue and yellow aftereffects are reported following longer exposures. There is no good evidence that McCollough hues are not complementary to the inducing hues or that the red/green opponent system is involved in a special way in the McCollough effect.

2.4.6 A site of chromatic adaptation precedes the site of the McCollough effect

As has been mentioned above, (section 2.4.3) McCollough and Clark (1970 unpub) found that alteration of the colour of one of McCollough's orthogonal gratings, (e.g. replacing the blue grating by a green one), affected the hues seen afterwards on both orientations of stripe on the test figure. This result might at first sight be directly explicable in terms of a population of McCollough's (1965b) "wavelength sensitive edge-detectors" of which the group left unfatigued and ready to be adapted by a grating of a particular colour will depend upon the colour of the immediately preceding grating. But Hirsch and Murch showed (1972) that such an explanation in terms of a single adaptation site is too simple. They found that the CIE values of the a-e hues could also be affected considerably without altering the colour of either grating by presenting an unpatterned differently coloured slide before the grating slide. When an orange grating (Wratten 16) was preceded by a yellow plain field (Wratten 74), and a blue-green grating (Wratten 47) was preceded by a blue field (Wratten 47B) - the four slides being presented for a few seconds apiece in succession a number of times, for a total of 6 min - the green a-e became more bluish and the yellow orange a-e more reddish than they had been in a control run in which the plain coloured fields were omitted. Hirsch and Murch (1972) conclude that these results and McCollough and Clark's require explanation in terms of "at least two levels in the visual system: first a "general color adaptation independent of edge detectors" which "selectively preadapts the color vision system", and secondly the "slope analysers".

Their next paper pressed home the same point (Murch and Hirsch, 1972). Here both inducing gratings were achromatic and differed only in the orientation of their stripes, yet being each shortly preceded (1 sec before) by a differently coloured unpatterned field, generated pattern contingent chromatic aftereffects. A chromatic effect was also induced using a single achromatic grating alternated every 10 sec with a single coloured field. The hues seen on the test gratings were the reverse of those produced by a normal McCollough exposure - as if the McCollough aftereffect were generated by the complementary afterimage of the coloured field. As in their previous paper, Murch and Hirsch account for these phenomena in terms of "the adaptive state of the retina at the time the inspection lines are presented". They assess the duration of this presumed selective fatigue of the retina by lengthening the time interval between presentation of the coloured field and of the achromatic inducing grating from 1-50 sec. With a presentation time for the coloured grating of 10 sec, the hue aftereffect became insignificant when the interval between presentations exceeded 20 sec. (The duration of the simple colour aftereffect following a 10 sec presentation of a bipartite red/green field is about 40-60 sec, VM.)

2.4.7 A colour opponent 'orthogonal inhibition'?

Several experimental observations raised the highly interesting possibility that the human visual system might contain an organisation (at or before the site of the McCollough effect), linking channels signalling orientations perpendicular to each other in a colour-opponent fashion. The evidence for this is set out below and also its interpretation in these terms. As will become clear in chapter 8, I consider this interpretation of the data to date to be ruled out by various control experiments. I have therefore indicated below in square brackets the points at which control experiments are instructive.

The idea of a "heterochrome and orthogonal inhibition between bar-detectors" was first suggested by an experiment of Hajos's (1970, 1973, fig. 2) in which he measured the saturation of the chromatic aftereffects (seen on a single vertical achromatic grating) after viewing: (a) a normal McCollough sequence of a green vertical and a red horizontal grating, and (b) on another occasion, the green grating alone. He was impressed by the fact that the saturation of the pink hue was much greater in the former case(by a factor of about 3)than in the latter and by the fact that doubling the time for which the green grating alone was viewed still did not greatly increase the pink aftereffect. He concluded that it was the horizontal red grating which was causing the large difference between the two runs, by producing a large red aftereffect perpendicular to itself. [A necessary control here is to omit the horizontal black bars from the normal McCollough inducing stimulus but not the red field. (see expt 8.1)] A control experiment on these lines was performed by Harris (1972) and showed that in the case of a <u>green</u> grating the orthogonal effect cannot be larger than the effect induced parallel to the grating. He viewed for 40 min a green grating presented alternately with an unpatterned red field, the green grating being rotated slowly throughout the inducing period so that it was presented equally at all angles. The aftereffect on a <u>single</u> achromatic grating presented at various angles was then found to be always pink relative to an unpatterned white field. Hajos (1971, 1973) performed a rather similar experiment also using green and not a red inducing grating. This too suggested (although he does not draw this conclusion) that any orthogonal effect produced by a green grating cannot be large. He employed an inducing regime similar to McCollough's (1965b) except that horizontal and vertical gratings were of the same colour (green). If there were any aftereffects of the opposite colour induced at the orientation perpendicular to each inducing grating these must be expected to reduce the saturation of the aftereffect on both vertical and horizontal test fields. Hajos plotted the strength of the aftereffect seen on a single grating presented at 10° intervals and remarked that the results for the two green inducing gratings used together were well approximated by the sum of the results for each green grating singly.

Curiously the red grating which, it had been alleged, produced "both a green aftereffect on the verticals and a red aftereffect on the horizontals of a neutral test pattern" (Hajos, 1971) was not further investigated and though the idea "that the colour-sensitive vertical and horizontal line detectors are organised in an opponent manner" was queried somewhat by Murch and Hirsch (1972) and by Harris (1972) it lived on and was invoked to explain two further phenomena.

Stromeyer (1969 Table 2) found that following exposure for 5-10 min to a single vertical coloured grating when one inspects (after simple chromatic effects have faded) a test field having areas of both vertical and horizontal achromatic stripes, the horizontally striped areas showed nearly as great a readiness to assume an illusory hue as the vertically striped areas. If one turns the test figure through 45° the hues disappear. [A control here is to substitute plain white test field for the vertical stripes - see Expt 8.1.]

The second phenomenon appeared to be a direct consequence of the previous one. It concerned the power of a grating apparently to 'neutralise' aftereffects at right angles to itself (Stromeyer, 1969, 1972; Murch and Hirsch, 1972). Hajos (1967) had found that the aftereffects seen on a two part test field (such as McCollough's 1965b) following a normal McCollough exposure to a red and a green grating could be reduced to zero by turning the inducing gratings through 90° and administering a second exposure, shorter than the first. By 1972 both Stromeyer (1969, 1972) and Murch and Hirsch (1972) were using this technique to "neutralise" or "disinhibit" unwanted residual aftereffects before commencing a new run, but whereas Hajos had used two gratings at right angles, they were using a single inducing grating. The implication seemed to be that exposure to a coloured grating produced an aftereffect of the same hue as itself at the orientation perpendicular to itself - in addition to the aftereffect in the complementary hue parallel to itself. Stromeyer (1969, Expt 2) expresses justified surprise that although the single grating when vertical "had originally produced a stronger aftereffect on the vertical grating than on the horizontal", the second exposure, to the same grating turned horizontal, can in one third the time "readily neutralise" these effects without producing "considerably stronger aftereffects on the horizontal grating than on the vertical". He concludes that "the interaction of processes due to orthogonal gratings is probably not additive". [Judging the 'neutrality' of the hues relative to a plain white field instead of relative to a second striped one is instructive here. see Chapter 8.]

The colour opponent orthogonal inhibition is further discussed in Chapter 3 and experiments to measure it following exposure to both red and green gratings appear in MacKay and MacKay 1977 and in Chapter 8.

2.4.8 McCollough effect visible at scotopic luminance levels

The phàntom fringes are said not to be visible at scotopic levels (Kohler, 1951; Hay, Pick and Rosser, 1963). These observers both reported that as the luminance of the visual field was decreased (within the range 40 mlm - 10^{-3} mlm) the fringes became more noticeable - being strongest "at about the level of dim electric light" (Kohler, 1951). But when the test luminance was further reduced, to that of "the colourless twilight" (Kohler, 1951, 16-17th day), "below the region of ordinary colour sensitivity" (i.e. below 10^{-3} mlm) "no colour fringes were seen". (Hay, Pick and Rosser, 1963, 10th day).

In the case of the McCollough effect, however, observations have been made which suggest that "colour sensations" can be "elicited through the rods" (Stromeyer, 1974), McCollough effects were induced at photopic levels (70ml) using a magenta and a green filter (Wratten 31 and 40 resp), a wide field (30°) and broad gratings so that the corresponding test gratings would be resolvable at scotopic levels. The exposures were either for 20 min to a vertical and a horizontal grating, (both of 0.75c/degree), or for 40-60 min to two vertical gratings of differing spatial frequencies (0.5 and 2.0c/degree). In both cases all three observers afterwards reported "pinkish" and "greenish" hues on the appropriate areas of paper test figures containing adjacent areas of suitable stripes, even when the luminance of the test gratings was reduced by means of a neutral wedge to a luminance level below 10^{-4} mlm. There seems no doubt that Stromeyer's observers were functioning at genuinely scotopic levels, for they noticed as the illumination was reduced that the test gratings changed their appearance markedly at just below 10^{-3} mlm from "sharp" to "diffuse". For two of the observers, dark adaptation curves were plotted using the same "yellow-green" illuminant, the same neutral density wedge and the same (though now unpatterned) white paper which had been used in the test gratings. The subject set the neutral density filter to such a position that as time proceeded "the 10° diameter disc of white paper on a black ground remained just below threshold". The "rod/cone break" in the resulting curves fell just below 10^{-3} mlm.

That these chromatic sensations can be elicited at scotopic levels of illumination indicates that either the cones themselves, or else those mechanisms which are usually fed by the cones, continue functioning at illumination levels where the cones are generally considered inactive. Stromeyer's interpretation of the results is that "rod signals influence colour mechanisms".

There is accumulating anatomical evidence of rod-cone interactions of various kinds even so early as the primary receptors in various animals (e.g. Dowling and Boycott, 1966). In man it has long been known that the twilight vision mechanism contributes to perceived hues at mesopic levels (Purkinje 1825) and there is increasing evidence of interaction at scotopic levels (bibliographies in: Trezona 1974; Frumkes and Temme, 1977). So this finding of Stromeyer's concerning the McCollough effect will possibly find a place in this context. If so, the site of the McCollough effect must be on the central side of at least one confluence of influences from rods and cones.

2.5 'Fatigue' and the McCollough effect - are there attendant reductions in visibility of coloured gratings?

Helmholtz (p235) describes two consequences of stimulation of the eye by light: firstly that sensation persists after the stimulation has ceased, and secondly that the sensitivity to further stimulation is lowered. This second aspect of the condition he calls "fatigue": "the fatigue of the nervous substance of vision has about the same effect on the sensation of fresh incident light as if the objective intensity of this light were diminished by a definite fraction" (p440). He had chiefly in mind the effects of viewing moderately lit static stimuli, but essentially the same explanation, invoking the fatigue of "organs" or "units" sensitive to various features of the visual world, has been extended to the effects of viewing coloured and moving stimuli (von Bezold 1876 p143; Barlow and Hill, 1963, resp). If the McCollough effect is indeed evidence, as Celeste McCollough suggested, of the 'adaptation' of wavelength sensitive 'edge-detectors' it might well be expected that the brightness and the visibility of gratings would be reduced by exposure to gratings of about the same colour, orientation and spacing.

2.5.1 Brightness reduction after McCollough exposure

Hajos (1970) says that a 25% reduction in the brightness of a striped field is produced by exposure to a green vertical grating. The subject matched the brightness of an unpatterned green field to that of a green grating before and after an exposure of "suitable length". (He does not appear to have published further details.)

2.5.2 Elevation of threshold following short exposures to coloured gratings

There have been several reports of reductions in the visibility of coloured gratings by brief prior exposures (lasting 120msec, 15sec, 3 min, 3.5min) to coloured gratings (May, 1972; Lovegrove and Over, 1973; Maudarbocus and Ruddock, 1973a; Sharpe, 1974 resp). It appears highly unlikely (see section 2.5.3) that these effects are ascribable solely to the McCollough mechanism. In sharpness of tuning for both angle and spatial frequency they show, as might be expected, resemblances to the parallel findings on achromatic stimuli (Blakemore and Nachmias, 1971; Blakemore and

Campbell, 1969b).

When exposure and test were administered to the same eye there was a colour specific elevation of threshold by a factor of at least 30% for all angles. When the orientation of adapting and test gratings came within about 15° of each other there was a marked increase in this difference to about 70%. This increase points to mechanisms sensitive to spacing and /or orientation which operate separately for the inputs to the red and to the green receptors. The bandwidth of this system is about 1½ octaves at 5 cycles per degree (Sharpe, 1974).

2.5.2.1 Interocular transfer of colour dependent threshold elevation?

Mandarbocus and Ruddock (1973a) and Sharpe (1974) have exposed one eye for about 3 min and tested on the other using similar sinusoidal blue and red gratings but have obtained differing results. The difference presumably stems from the fact that whilst Mandarbocus and Ruddock seem to have occluded (Mandarbocus, 1973) the unexposed eye, Sharpe "held a piece of ground glass" over his to maintain its state of light adaptation and so this eye was receiving light of the same colour as the exposed eye. During testing the ground glass was placed over the other eye. Mandarbocus and Ruddock (1973a) found no colour specific difference in threshold elevation (and a 1 octave bandwidth for the effect). Sharpe (1974) on the other hand found a 30% colour specific difference in threshold elevation; transfer to the unexposed eye was 84% when the colour was different in adapting and testing and 54% when it was the same. This difference may be ascribable to simply the colour adaptation of the 'transfer' eye as a result of looking at coloured light through the ground glass or to the dichoptic mechanisms of chapter 6.1.5.

2.5.2. What is not clear, as Timney, Gentry, Skowbo and Morant (1974, 1976) pointed out - is the extent to which the McCollough mechanism is responsible for any or all of the above reductions in visibility. The inducing times used were short (120msec - 3.5min) and in no case was it reported that subjects could see a McCollough aftereffect. Timney et al (1974) found that after exposure to a coloured grating for 50 min, though "there was a pronounced elevation of threshold immediately following adaptation, it is usually back to base level within 30 min". At the end of this time a McCollough effect was, however, still visible (and presumably quite distinctly so after so long an inducing period).

2.5.3 Threshold measurements when a McCollough effect was known to be present

Timney et al (1974) therefore sought to isolate the effects of the McCollough effect from those of other shorter-lived effects by allowing half an hour to elapse after the end of the McCollough exposure before making threshold measurements. These were made at 11 wavelengths evenly spaced from 500-630nm. They also measured the strength of their subjects' McCollough effects before and after performing the threshold measurements. A very long (90 min) McCollough exposure (at 620nm and 530nm) ensured that a considerable aftereffect (38% saturation) was present. Their plots of threshold as a function of wavelength before and after the McCollough exposure are almost coincident. And their conclusion is that "the sufficient conditions for generating and sustaining a McCollough effect are not adequate to produce or maintain an orientation-specific threshold elevation".

2.5.3.1 Kruger (personal communication 1976) has, pointed out that such differences as there are between their two plots, though small, are systematic. These suggest that visibility was actually increased (by about 7%) for the test grating whose colour and orientation coincided with that of the inducing grating, though it was decreased throughout much of the spectrum.

2.5.3.2 In summary, though considerable colour and orientation specific threshold elevations have been recorded shortly after viewing coloured gratings these are not definitely ascribable to the McCollough mechanism.

2.6 Areal specificity of the McCollough aftereffect

The McCollough aftereffect can generalize at reduced saturation over a few degrees of a uniformly striped test area which overlaps part of the area stimulated during induction of the effect (Murch, 1969; Stromeyer, 1972a). "When the pattern ($6\frac{2}{3}^{\circ}$ square) partially overlapped the marginally larger adapted area, no subject reported seeing a sharp border between an area of colour and an area of no colour on the test pattern, although the aftereffect appeared more saturated on the adapted side." (Stromeyer, 1972a). When the test field contained areas of differently oriented stripes the colour spread out to the nearest border and stopped there. (Harris and Barkow, mentioned by Harris, 1970.) The hue was judged most saturated when the test area "largely overlapped the adapted area" (Stromeyer, 1972a). When the entire test pattern fell more than 40' of arc outside the area of the visual field previously occupied by the inducing grating no effect was seen (Stromeyer, 1972a).

Strict fixation during both induction and testing of these effects is, of course, essential. In the tests which led Murch (1968, 1969, 1970) to claim that the aftereffect extends over the whole test pattern the subjects were given no fixation point or instructions during testing.

Stromeyer (1972a) and Harris (1970) both suggest that small involuntary eye movements may lead to the limited degree of generalisation, which they have observed. Harris (1970) alludes to the well-known tendency of "a shallow gradient of brightness or colour within a bounded region to yield a homogeneous appearance throughout that region".

2.6.1 <u>Generalisation across the vertical mid-line of the visual field?</u>

Murch (1974a) has raised the interesting question as to whether generalisation occurs across the midline of the visual field. Stromeyer's (1972a) fixation points during (binocular) induction and testing of the McCollough effects were at the midpoint either of the top edge or of the left-hand edge of the pattern and in reducing the degree of overlap he moved the probe upwards or leftwards respectively. In the case of leftward movement the input from the test probe was therefore "shifted from the right to the left lateral geniculate body which had not been adapted for colour during induction" (Murch, 1974a). In fact, such small differences as there are in Stromeyer's results tend to suggest that there is less generalisation vertically than horizontally! Murch performed a similar experiment monocularly asking his 12 subjects to fixate with their left eye the middle of the test pattern and to indicate "whether the colour covered the entire test pattern or only a portion of it. In the group for whom the test field had moved vertically (i.e. remaining within the same hemi-retina) only a minority reported a hue difference, and "indicated that the border was very unspecific" whereas in the case of horizontal movement all subjects "who reported an appropriate hue on the test pattern also reported that the colour covered only part of the test pattern" and a "distinct border" was indicated. The difference here hangs on a 9:3 difference in the reports by the nine different subjects in groups "1b" and "2b". Slightly longer exposure durations, (7 min was used), the use of the same groups of subjects under both conditions, or else of much larger groups could have put this highly interesting matter beyond doubt. Stromeyer, as mentioned above, had found no difference and a different approach by Murch to the same question (see below) yielded no definite support for Murch's idea that the McCollough effect generalises within each hemi-retina but not across the vertical midline.

Murch's (1974a) second approach to this question of generalisation across different parts of the retina or brain was an adaptation of an experiment by Harris (1969). Harris had reported that "different aftereffects were produced simultaneously on adjacent retinal regions" (to left and right of a fixation point) by opposite pairing of colour and orientation in the two regions during induction. Murch obtained subjective scores of the aftereffect's strength from 11 subjects on two occasions a week apart. For the first inducing exposure the field was divided vertically and for the second horizontally into two areas in which colour and orientation were oppositely paired. There was no significant difference between the subjects' reports on the two occasions. This result suggests that there is no greater degree of smudging or generalisation within the two halves of the brain than occurs across the midline.

2.7 Size scaling and Emmert's law

If one views a person, or indeed any familiar object from various distances, though they look smaller when they are further away, their apparent size is not diminished in proportion to their distance. Even the apparent sizes of unfamiliar objects are adjusted at distances up to about 2 metres presumably on the basis of cues as to their distance derived from accommodation, convergence and probable surface texture. This 'size scaling' is obviously a subtle and complex correction and probably the product of fairly central processing. If 'size scaling' did not operate for a particular visual object and instead the apparent size of the object corresponded exactly to its retinal dimensions the apparent size would, of course, diminish in proportion to its distance from the observer. Such a relationship is expressed by Emmert's law. The ordinary Hering after image of a luminous object - for example the sun - obeys Emmert's law. It occupies the same region of the visual field as the original luminous stimulus no matter how distant the background against which it is later studied. This absence of subtle corrections suggests that this aftereffect is largely the product of modifications at or fairly near the retina.

Turning to the McCollough aftereffect it has two aspects upon which size scaling might operate: (as in the case of the Hering afterimage) there is the 'size' of the area within which the aftereffect is seen and there is also the 'size' of the grating spacing which elicits the strongest aftereffect.

2.7.1 Size scaling of the area occupied by aftereffect

Murch (1968, 1969) attempted to find the area occupied by the McCollough afterimage when the test gratings were presented at distances of 2-8ft. As has been stated in the previous section, he gave his subjects no fixation instructions for the test sessions nor fixation point to hold onto visually whilst they decided to which numbers along the sides of the test field the coloured effects extended. His conclusion that "coloured areas always extend to the borders of the lined area of the test pattern" (1969) is probably therefore valueless. For wherever the subject turns his fovea to see whether a colour is present and to read the numbers, the colours would immediately appear on any horizontal or vertical lines.

2.7.2 Size scaling of the grating spacing

Harris (1970) was interested in the second question - whether the strength of the McCollough aftereffect colours depended upon the true or the apparent angular spacing of the stripes of the test fields. In a preliminary experiment he found that "seven subjects placed photographic prints of achromatic gratings at a distance which suggests that the McCollough effect obeys Emmert's law". (The room in which the subjects viewed the prints was lit by "dim incandescent light" so that the distances of the prints could be judged and size scaling operate upon their apparent size.)

Since the strength of the McCollough effect does not peak at all sharply as one alters ones distance from a stationary test field, Harris devised a more sensitive technique. He exposed subjects to two vertical gratings of differing spatial frequencies (e.g. magenta 10 cycles per degree, and green 5 cycles per degree presented alternately at 60cm for a total of 30 min). He then asked them to adjust by means of pulleys the distance of each of a set of prints of an achromatic grating at differing magnifications until in each case the colour was "neither pink nor green". This method has the merit that the judgement will be unaffected by the fading of the aftereffect with time, but the disadvantage that the retinal subtense selected for the crossover point will not correspond directly with either of the retinal spacings used to induce the effect. The 7 subjects' settings by dim incandescent light fell in the range 30-190cm and produced straight line graphs corresponding to an angular subtense of 7-9.7 cycles per degree. This, though high, especially on an octave (logarithmic) scale is not an impossible value for the crossover point. And since perfect size constancy would be expected to yield reports that hue was unaffected by distance and that no null point was obtainable, Harris's results do point away from size constancy. He concludes that "the crucial thing for the McCollough effect is retinal stripe width".

2.8 Site of the McCollough effect relative to those of other visual processes

2.8.1 The fading of stabilised images

Coloured gratings which are stabilised in retinal position do not induce a McCollough effect (Piggins and Leppman, 1973; section 2.3.2). This suggests that the locus of the fading of the stabilised images precedes the locus of the McCollough mechanism.

2.8.2 Pressure blinding

So far as I am aware, induction during pressure blinding has not yet (1977) been attempted.

2.8.3 'Ordinary' chromatic adaptation

The experiments of Murch and Hirsch (1972, section 2.4.6) show that the site of the McCollough effect follows that of the ordinary shift in spectral sensitivity which lasts for 20-50 sec after viewing a coloured light for 10 sec.

2.8.4 Simultaneous colour contrast

Stromeyer (1971) constructed a test figure of thirty six $3\frac{1}{2}°$ squares in various shades of grey, each patterned with five horizontal or vertical achromatic bars of a different contrast. Subjects with a very strong McCollough effect (produced by 2 hours' exposure to magenta and green gratings, Wratten 31 and 40 resp) viewed this test array at mesopic luminance levels and found that the squares took on hues which depended not simply upon the orientation of the bars, but also upon the more subtle effects of added grey and simultaneous contrast with adjoining squares. Munsell colour 'chips' were selected by the subject (using his other eye and the prescribed Munsell lighting) as matches to the perceived hues. A wide range of colours were selected, some - particularly the blues and greens - at high saturations. Stromeyer compares the chromaticities with those recorded for the Land effect and only the oranges, reds, pinks are less saturated than in the Land effect.

These findings suggest that the site of the McCollough effect precedes the mechanisms of simultaneous colour contrast.

2.8.5 The spatial frequency shift illusion

Stromeyer's (1972b) experiment has already been described (chapter 1.6) in which a spacing contingent chromatic aftereffect became visible on a grating of intermediate spatial frequency only when a spatial frequency shift had also been induced. The inference from this would seem to be that the site of the McCollough effect follows a site of the spatial frequency shift in the monocular channel, but his observations on the lack of chromatic effect in the other eye (which had not been exposed to the Blakemore and Sutton (1969) stimulus) shows that the site of the interocular transfer of the spatial frequency shift comes later than that of the McCollough effect.

2.8.6 The tilt illusion

Mikaelian (1976) asked the interesting question as to whether the site of the large tilt effect (inducible by walking around wearing prisms which tilt the whole visual world through about 40°) precedes the site of the McCollough effect. He sought to test whether it is the true retinal orientation of the McCollough inducing stripes or their "corrected" orientation as perceived during induction (wearing prisms) which determines the orientations at which the McCollough aftereffect has its maxima. Mikaelian's conclusion is that it is the perceived and not the retinal position that is the decisive factor. It is difficult to know how to assess this conclusion since Mikaelian did not measure the remaining tilt after the 4 min of McCollough exposure or after the setting of achromatic gratings to the orientations at which they appeared most strongly coloured. Unless the tilt aftereffect decays between the time at which the subject is receiving his McCollough effect and the time at which he makes the settings of the test gratings for maximum chromatic effect, there can be no possibility of distinguishing between the two hypotheses. In each case the subject will set the test field stripes parallel to the original true orientations of the inducing field i.e. vertical and horizontal. Only when the tilt aftereffect has worn off somewhat can an appreciable difference be expected. It is therefore odd that Mikaelian (a) has his subjects make their chromatic settings straight after exposure to the McCollough stimuli, and (b) that he gives no indication of how fast the tilt aftereffect is disappearing at that time.

Redding (1975) gives decay curves for what is substantially the same effect (though his subjects were explicitly forbidden to use or to look at their hands whilst walking around corridors for 48 min wearing 30° tilt prisms). These curves enable one to guess likely values for the tilt at various stages of Mikaelian's experiment. Guessing that Mikaelian's subjects took at least two minutes to make their tilt setting and then "move to a chair facing the projection screen for viewing the McCollough inducing stimuli", the difference to be expected on the two hypotheses for a subject with an initial tilt of 10° is at most about 5°. In view of the breadth of tuning of the McCollough effect such a small difference is not easy to detect reliably.

Ellis (1976) has performed what he sees as a related experiment, and from it concludes that, when due allowance has been made for the (photographed) counter-torsion of the eye, the McCollough effect is "retinally locked" and exhibits no orientational constancy. He is, however, not dealing with the same situation as Mikaelian. Mikaelian's subjects had, through prolonged locomotion wearing tilting prisms, 'learned' a new association between visual and gravitational orientations. Ellis's were not subject to any discrepant clues as to gravitational or visual vertical; they simply viewed tilted inducing gratings with upright head and upright inducing gratings with (20°) tilted head.

2.8.7 Cognitive Contours and also the Gibsonian tilt effect

A.T. Smith (personal communication of work performed in 1974) has tried to produce a McCollough effect using subjective contours, but obtained no significant effect. But it is interesting that he was able, using the very same type of stimulus, to induce a sizeable Gibsonian tilt effect (Smith and Over, 1976, 1977).

2.8.8 Cyclopean vision

Julesz (1971, p263) reported that "an attempt to localise the McCollough effect by Cyclopean techniques by Stromeyer and myself failed". They were exploring whether the colour biassed output from the McCollough mechanism could assist in stereoscopic fusion. Julesz says that when real colour was presented to one eye in the small areas corresponding to striped achromatic zones in the other "some fleeting moments of fusion" were observed. He puts down the general failure to obtain fusion under various rivalrous conditions to the low saturation of the McCollough hues.

2.8.9 Visually evoked potentials

May, Leftwich and Aptaker (1974) have reported that the amplitude of the visual evoked potential "is reliably diminished in situations where S adapts to and is tested with gratings of the same wavelength and orientation".

The scalp potentials were evoked by vibrating the test grating through one bar width at 7Hz. The adaptation was for 20 sec.

In view of Timney et al's (1974) report that there is no long term threshold change following short exposures to coloured gratings, they are cautious about ascribing the changes in EP amplitude to the McCollough mechanism. Their conclusion is that "the results obtained previously (i.e. May, 1972) and in the present investigation depend upon a local retinal adaptation which is quite transient in nature".

2.8.10 Gestalt Perception

Jenkins and Ross (1977) have reported that when a subject with a McCollough aftereffect shifts his perception of a set of symmetrically nesting squares so that the figure is perceived as four triangles the aftereffect hues alter in strength. The hues are weaker or even absent when the figure is perceived as a system of squares.

Control tests (see Appendix III) suggest that the phenomenon they describe is of wider applicability and not especially a property of the McCollough effect.

2.8.11 Hemispheric differences

Myer (1976) has obtained verbal reports from 3 right handed subjects that the McCollough effect looks stronger when the test pattern is presented in that part of the visual field which is processed by the right hemisphere. (see 2.8.4.3)

2.8.12 Imagination

Finke and Schmidt (1977) claim that significant orientation contingent chromatic aftereffects have been induced in 89 subjects by asking them to 'imagine' colours onto achromatic gratings or black bars onto unpatterned coloured areas. I obtained no measurable or visible effect myself in 1973 after 20 min spent in similarly imagining colours.

A summary of those features of the McCollough effect which appear to me to be the most interesting as regards its mechanism and site appears in Chapter 9.

2.9 Supplement to literature review: Summary of methods that have been used for induction, testing and measurement of McCollough aftereffects

There are generally two parts to an experiment on the McCollough effect: exposure to stimuli which may induce an effect and subsequent inspection of suitably patterned test fields.

2.9.1 Presentation of the inducing stimuli raises no problems: they may be presented on a screen by a projector in a darkened room or in a tachistoscope or even printed on paper to view by daylight, as was once done on the cover of the 'New Scientist'.

2.9.2 But if one wishes to induce as large as possible an effect in a given time the following guide-lines may be extracted from the literature:

2.9.2.1 Two orthogonal gratings in roughly red and green colours should be presented alternately (Hajos, 1970; Stromeyer, 1972).

2.9.2.2 The grating spacing should be 2.5-10 cycles per degree (Stromeyer, 1972).

2.9.2.3 The contrast of the patterns should be as high as possible (Harris and Barkow, 1969). K. Castellan, 1976 and K. White found that the aftereffect strength increased with increasing luminance up to 30ft lamberts.

If aftereffects dependent upon luminance and contrast are not to be also induced (Mayhew and Anstis 1972; Heggelund and Hohmann 1976) the stripes of the two colours should be matched in intensity.

2.9.2.4 The duration of the separate presentations of the red and the green grating should be about 3-60 sec (White and Ellis, 1976; K. White, 1975). Dark intervals between these presentations may, without loss, be of several seconds' duration (Hajos, 1967; K. Bradshaw, 1977).

2.9.2.5 The total duration of the induction should be in the region 5-30 min (Hajos, 1967).

2.9.2.6 The subject must not roll his head about, or otherwise change the tilt of his retina relative to the orientation of theinducing gratings (Ellis, 1976). He should, however, be encouraged not to fixate, or simple after-images will form. He may be instructed to scan each grating in an identical (circular) fashion changing direction now and then so as to eliminate systematic effects of eye position and eye motion. This activity also helps him to maintain focus and to combat boredom and the closing of the eyelids to sleep.

2.9.3 Testing the aftereffects

2.9.3.1 The aftereffect hues are most clearly seen on a bipartite field with abutting areas of pattern. They are strongest when this bears patterns at the same orientation* and of the same angular subtense at the subject's eye as those used to induce the effect (Harris, 1970).

2.9.3.2 The hues look strongest at rather dim (mesopic) levels of illumination of the test card. (·1-100 cd/m^2, Stromeyer, 1971; Stromeyer and Dawson, 1974, p778; 2cd/m^2, VM unpublished).

*This is not strictly true for all arrangements of inducing gratings (see experiment 8.2.1, 8.2.2).

2.9.4 To obtain a measure of the strength of McCollough aftereffects various methods have been employed:

2.9.4.1 The subject may be invited to name the hues he sees on the test field,the proportion of 'correct' reports being used as the measure (Hajos, 1967). This method is obviously applicable only in the region of threshold. Keys, Hensley and Matteson(1974)used it to obtain from 23 subjects two plots for the angular spread of the aftereffect of a single green and a single red grating which agree well with Hajos's (1970) plot obtained using a colour mixer.

2.9.4.2 To ask the subject to indicate the angle of tilt of the test figure at which hues are no longer visible (Teft and Clark, 1968). This indirect method had no exact meaning until the angular tuning curves for various grating spacings and aftereffect strengths had been determined by other means..

2.9.4.3 To invite the subject to give a numerical rating, S.S. Stevens-style, to the colours he sees. (Fidell, 1967; Stromeyer, 1969; Uhlarik and Osgood, 1976; Myers, 1976). The large scatter of Fidell's results is not necessarily a reflection on this method, which in other contexts has given remarkably reliable results, but may be put down to the smallness of her seven groups of subjects, and their being permitted to set their own completely personal number scales.

The use of this method to establish hemispheric differences, (Meyer, 1976), is not ideal, since one half of the brain is likely to be more strongly involved than the other in the ascription of numbers as ratings.

2.9.4.4 Hue matching

To invite the subject to select from a range genuinely tinted areas those which best match his aftereffect hues (Hajos, 1970; Stromeyer, 1972b, 1971; MacKay and MacKay, 1973, 1975, 1977; Skowbo, Timney et al, 1975). This method is direct and involves the minimum of verbal involvement and allows a record to be obtained of what the subject was seeing from which chromatic purities can later be worked out, if desired. The coloured areas may be either Munsell chips or a region of the test field illuminated by a colour mixer. Hajos (1970) built two colour mixers, (one for the pink and one for the green a-e) each having a trio of projectors containing a red, a green and a white filter. The red and the green filters were different in each mixer (and different again from the inducing filters). This probably means that although his colour matching may have been very good, the scales for measuring his red and his green after effects were probably not identical. As the bulbs in the six projectors aged and had to be replaced his measure of saturation will have been disturbed.

MacKay and MacKay's simpler mixer which uses a single projector for matching both green and pink aftereffects is described briefly in the next chapter and is described and discussed in detail in Chapter 4.2.

Shute (1977a) has described an arrangement for measuring the McCollough effect using two slide viewers. One is for presenting a test slide with two orientations of grating and another for producing coloured light of a single colour at a known saturation. This saturation is adjustable by the subject to match that of his pink aftereffect.

Skowbo, Gentry, Timney and Morant (1974) used a tristimulus projection colorimeter "modeled after a design by Riggs, 1964". This enabled "colour matches to be converted into CIE x, y coordinates". The "homogeneous chromatic field seen with the right eye was adjusted to match the McCollough hues seen on the test gratings viewed with the left".

2.9.4.5 Hue cancellation

Riggs, White and Eimas (1974, and White 1976b) constructed an elegant colour mixer in which the hues of the two orthogonally striped halves of their test field were simultaneously alterable by a single rotatable control. As the proportions of red to green light in the mixture in one half decreased, so they increased in the other. The subject was invited to turn the control until both his aftereffect hues were cancelled and the two half fields "appeared matched" at a near achromatic hue.

The control rotated a disc bearing a regular matrix of small squares of superimposed polaroid and colour filter in two complementary colours. These were so paired that when light from a single projector had passed through them it was coloured magenta and green in two planes polarised mutually at right angles. (A steady white unpolarised illuminant was added, to suitably dilute the hues.) The backs of the two halves of the test field bore polaroid at two mutually orthogonal angles.

This means of measurement has the merit that when the subject has completed his match setting, the test card looks (almost) the same to him whatever his aftereffect strength (a Class 1 measurement). It has the disadvantage that he is then in fact receiving stimulation from a large field of coloured oriented stripes which will certainly generate a small new opposite McCollough effect. Keith White (1976) reports that measurement did not affect the overall course of decay.

The apparatus has two very pleasing features. The first is the achievement of uniform colour mixing by the use of the array of small squares of colour filter. The second is the fact that any difference in the transmissive power of the two colour filters should be immediately detectable from a variation in the luminance difference between the two halves of the test field as the disc is turned through its range.

Jones and Holding (1975) constructed a similar colour mixer on advice from Keith White, but appear to have presented only one orientation of test grating to any one subject (p.324) and to have used no comparison field (see Chapter 5.1.5, 5.7).

CHAPTER 3 SOME OPEN QUESTIONS 1972-1977:

An Introduction to the experiments

3.1 Two Overall Questions

Celeste McCollough (1965) suggested that both the aftereffect which she had discovered and the "phantom fringes" had their origin in the 'color-adaptation of edge-detector systems'. This phrase at once presents two major questions concerning the McCollough effect: where in the visual pathway are these systems located? and what is the nature of the adaptable systems? (e.g. are they fatig able cells or modifiable networks of cells?). The literature reviewed in the preceding two chapters has shaped and eliminated answers to both questions and the purpose of this thesis has been, if possible, to continue the process. Thus, for example, the measurements of the aftereffects in each eye following various exposures of the two eyes to differing, conflicting and concurring combinations of colour and pattern were undertaken with the question of locus particularly in view. The studies of the growth and decay of the aftereffect and especially of the susceptibility of the decay process to external factors were directed to the question of mechanism. The work on the angular distribution function began as an investigation of an alleged orthogonal opponent-colour aspect of the mechanism, and resulted in a considerably simplified view of the mechanism not only of the McCollough effect but probably of curvature and angle-sensitive chromatic aftereffects too.

There is another aspect of the question of mechanism which the literature has already brought out and which almost forms a separate question: it is whether the 'edge-detector systems' chromatically 'adapted' to give the McCollough aftereffect are different from the systems which are 'adapted' in a number of achromatic aftereffects which also involve orientation and spacing of patterns. Only by crisp delineation of the properties of each aftereffect will the differences and the coincidences become clear. It is hoped that the work on the time course, the retention in darkness, the angular spread and the binocular aspects of the McCollough effect will, by providing "finger prints" of the McCollough effect,assist in the making both of identifications and discriminations.

These questions of site and mechanism presuppose eventual answers in terms which will be largely anatomical and neurophysiological, and indeed one ambition of psychophysical work is to build up a description of internally perceived effects sufficiently clear and complete in critical respects that eventually a particular neural state or activity may be pointed to as their correlate. The building of such a bridge between internal experience and observable neural activity is obviously only a future aspiration. It has however given rise to at least one emphasis in this thesis: the stress on temporal factors in the McCollough effect springs from the conviction that time patterns are almost the only measurable feature which will appear in unequivocal form on both sides of the bridge.

Beyond this hoped for identification of a particular local brain state and brain activity as the correlates of 'having' and seeing a McCollough aftereffect there lies a still more interesting question for the future: what part does this biassed activity play in the functioning of our vision as a whole? Is the bias only 'fatigue', or is it a useful adjustment to a changing environment which - like 'dark adaptation' for example - serves to optimise the system's performance? This thesis does not set out to answer these questions but they cannot but be mentioned here since they have influenced the overall direction and mode of exploration in all that follows.

3.2 The time constants of the McCollough effect

3.2.1 The Decay Course of the McCollough effect

The McCollough effect is remarkably long-lasting. The fairly strong hues which are seen on achromatic gratings immediately after an inducing exposure diminish rapidly for the first 15 minutes or so spent under ordinary lighting conditions, but the pale pastel hues then seen continue for the remainder of that day and most of the next with almost imperceptible fading. This duration is so unlike that either of ordinary* visual aftereffects (see table 1) on the one hand or of the recovery times reported for single cells (Adrian, 1928; Barlow and Hill, 1963b; Horn and Hill, 1969; Svaetichin, Megishi and Fatetichand, 1965), on the other, that it seemed to point to something interesting about the mechanism of the McCollough effect which could perhaps be clarified by closer study of the time course of decay.

To measure the strength of the McCollough aftereffect the simple and direct method was employed of asking the subject at intervals to make hue matches to the chromatic aftereffects which he could see on achromatic gratings presented at the two mutually orthogonal orientations used during induction. The adjustable hue was provided by a colour mixer which by linear displacement of 2 abutting filters altered the red/green balance of part or parts of the test field while keeping their intensity constant. A convenient measure of the subject's McCollough effect at any moment was then the displacement of the filter when the subject passed from his hue match to an achromatic grating at one orientation, to that at the other

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* By 'ordinary' I mean to exclude those aftereffects which involve learned visual-motor co-ordination and the contingent aftereffects.

appropriate orientation.

Using this measure of the McCollough aftereffect, we found that recovery after a McCollough exposure is not exponential (as would be the case for a process in which the fractional rate of 'repair' is independent of the time at which repair occurs) but becomes progressively slower as time proceeds (Expt. 5.1.1). A log/log plot of the aftereffect against time measured from the end of the McCollough exposure gave not only a straight line which fitted the data fairly closely (MacKay and MacKay, 1973; Riggs, White and Eimas, 1973), but also yielded rather similar slopes for a range of induction times.

3.2.2 Factors which alter the rate of decay

We felt that if any factor could be found to affect the decay rate of the McCollough effect, this would be a source of clues as to the underlying mechanism.

First, various aspects of the inducing stimuli were altered, but without noticeable effect: binocular exposure to contrary stimuli was used with the possibility in mind that binocular interaction between the opposing aftereffects in the two eyes might hasten decay (Expt 5.1.1 and 6.3): red and green gratings were used singly (Expt 5.1.2) and orthogonal blue and yellow gratings were paired together in case the various colour channels were differently involved. The repeat rate of the inducing cycle was made as rapid as the apparatus then allowed with the idea that briefer individual exposures might give rise to less well consolidated effects. (Keith Bradshaw, 1978, who later took over the study of timing as an influence on the decay of the McCollough effect did later find, that with 'on' times of below 1 sec, the aftereffect was weaker and decayed more rapidly.)

Secondly, factors following induction were investigated, but neither a bleach from which vision took 12 min to recover, nor hours spent at the widely differing luminance levels of summer daylight on the one hand and indoor lighting on the other made any significant impression on the steady process of decay. This is not to say that modest fluctuations in slope did not occur from day to day, but they seemed uncorrelated with the subject's visual diet, and perhaps - if anything - reflected his gastronomic diet and tiredness. The differences between subjects were not much greater than these 'random' fluctuations found in a single subject. All together it began to seem likely that recovery from a McCollough effect was an endogenous process not readily accessible to external manipulation.

A curious feature, however, of runs which extended over into a second day repeatedly emerged; an aftereffect which looked weak and faded in the evening appeared freshened and more colourful the following morning. The measurements showed the same feature, being, after breakfast, as much as 10% above the previous evening's last reading and thus 40% above the level that would have been predicted by extrapolation of the previous day's falling slope through the hours of night. This seemed a strange kind of recovery from 'fatigue', and it raised the question as to how much of this increased effect was attributable to refreshed signalling of the features of the test field by parts of the visual system peripheral to the McCollough mechanism, and how much to the state of the McCollough mechanism itself. To separate these two factors, an aftereffect was induced shortly before shutting the eyes for the night (Expt 5.4.1) and its decay followed throughout the next day until long after any morning freshness might be supposed to have evaporated. Not only the early morning readings, but the entire course of the resulting graph fell well above that predicted from the previous evening's starting level on the assumption that mere passage of time produces decay. The strength and rate of fading of the chromatic effects during the day took values similar to those taken by an effect newly induced in the morning. In short, the night hours seemed to have wrought no recovery at all (MacKay and MacKay, 1975b, 1977a).

These results at first suggest that a complete "freeze" of the McCollough mechanism occurs during darkness, but other runs in which more decay had occurred before the dark period did not fit with so simple a hypothesis (Expt 5.5. and 5.5.1). On occasions when the decay of an aftereffect induced in the morning was followed through a second and even a third day, the results from the later days did not fall on the extrapolation of the first day's graph,even when the hours of night were omitted before plotting. If, however, the time of waking on each later day was taken as a fresh time origin, a log/log plot of slope similar to that of the first day was obtained. Further runs were designed to test whether after a period of darkness shorter than a whole night the rate of decay of the McCollough effect resumes where it was interrupted by darkness, or is more rapid. The arrest of the decay of the McCollough effect during sleep and darkness turned the question as to factors influencing the decay rate on its head - the question became how is a McCollough bias, once induced, ever lost? Was light alone sufficient to produce recovery, or was patterned light essential (Expt 5.3.2)? Did recovery occur if one was in the dark but awake? Unpatterned light proved to be the essential factor, being as effective as the ordinary environment in removing an aftereffect (MacKay and MacKay, 1975b; Skowbo, Gentry, Timney and Morant, 1974). Continuous viewing for 20 min of achromatic gratings was even more effective (MacKay and MacKay, 1975b and Skowbo et al 1974) but this effect was slightly reversible and so in part at least the result of other aftereffects induced by these gratings and overlying the McCollough effect (Expt 5.3.3.1).

The next question was how did the decay rate depend upon the amount of light entering the eye? (Expt 5.4.4.1). As has been mentioned already, the log/log slope of decay did not seem to be significantly different for runs for which the environment was rather poor indoor lighting and runs when most of the recovery time was spent out doors in light some thousands of times brighter. Runs, however, in which an interference filter and a neutral density filter were worn on the 2 eyes to study whether the recovery rate was affected by the wavelength of the incoming light revealed that at lower luminance levels the recovery rate was less rapid irrespective of wavelength. The dependence of both induction (ch 5.8.3) and recovery (Expt 5.1.8) rates upon the intensity of the light entering the eye was investigated wearing artificial pupils. The scotopic range was included in this investigation since the McCollough aftereffect was known to be visible well below the rod/cone break (Stromeyer 1974).

In 1975 it was suggested by Jones and Holding that it is the viewing of a achromatic grating which starts the decay process and that in the absence of testing there was little decline in the aftereffect over 5 days and more. Attempts were made to replicate (Expt 5.6.1.1) and then to account for their observations.

3.2.3 Additivity of earlier and later aftereffects

The power law of decay implies, of course, that the rate of decay does not depend simply upon the magnitude of the effect at any given moment. For example the aftereffect of a long exposure administered to one eye several hours previously may have the same magnitude as the aftereffect of a brief exposure given to the other eye 5 minutes ago but their rates of decay will be very different (by a factor of about 20).

The question as to how such aftereffects combine if administered to the same eye was investigated in hopes of gaining a clearer picture of the mechanisms involved (ch 5.7).

3.2.4 The Growth of the McCollough effect

It was noticed that subjects whose aftereffects decayed at the same rate nevertheless took widely different (x5) times to acquire effects of comparable strength. The growth process was investigated (Expt 5.8.1) in the hope of finding how growth and decay of the aftereffect are related.

3.3 Binocular involvement in the McCollough effect

3.3.1 Dichoptic induction

Since the McCollough effect does not transfer detectably to an unexposed eye (McCollough, 1965b), an interesting question (actually suggested to my husband by Stuart Butler of Birmingham in 1972), was whether a McCollough aftereffect can be dichoptically induced, i.e. whether chromatic effects contingent upon pattern are induced if one 'shares' the McCollough stimulus between the two eyes so that at the same times that red and green unpatterned fields are alternately presented to one eye, achromatic gratings at two orthogonal orientations are alternately presented to the other. If so, it is difficult to imagine - unless efferents to the retina are discovered - that the site of the mechanism producing such a dichoptic effect can be more peripheral than the lateral geniculate body, where fibres from the two eyes first approach each other. We found after 10-15 min of dichoptic induction that both eyes did see coloured aftereffects upon striped achromatic test fields, though the hues were considerably weaker than after the same length of monocular exposure.

The hues were opposite for the two eyes. The eye which had been exposed to unpatterned colour saw hues on the test field complementary to those which had been paired with each orientation during induction of the effect, i.e. it saw a normal, though weak McCollough effect. The eye which had been exposed to achromatic gratings, on the other hand, saw illusory hues on the test field in the same colour which had been paired with each orientation during induction (MacKay and MacKay, 1973, 1977a and Expt 6.1.1).

To account for the latter 'anomalous' McCollough effect one might propose that between the two eyes there operates a colour normalising system such that white light is, for example, taken to be slightly green when red light is flooding the other eye. In this case a further question arises as to how globally or locally such colour normalisation occurs? Must the whole retina, or at least the two half-retinae feeding the separate cortical hemispheres be receiving a unanimous colour input or can dichoptic effects still be induced when the upper and lower halves of a retina simultaneously receive oppositely coloured inputs? (Expt 6.1.7.1). A similar question as to whether it is the pattern or its 'negative' which is transferred to the non-pattern viewing eye was investigated using spots instead of stripes but unfortunately without conclusive outcome as the effects were too small.

An important question concerning the dichoptically induced McCollough effect was whether it is essentially the same effect as the ordinary McCollough effect, in the sense of being evidence of an identical process of adaptation or modification. The colour mixer for matching the after effect hues was built to enable the time courses of growth and decay and spatial frequency dependence to be compared for the two aftereffects (MacKay and MacKay, 1975a and Expt 6.1.1). These three properties are characteristic, of course, of the entire visual path which includes the modifiable elements responsible for the pattern contingent chromatic aftereffects. The long decay of the McCollough effect and its retention in darkness, however, permits its temporal aspects to be distinguished from those of the other effects of viewing the coloured, tilted inducing gratings and thus provides a fairly unambiguous 'finger print' of the aftereffect.

3.3.2 Interocular Transfer of the McCollough effect

The existence of a dichoptically induced ingredient in the McCollough effect made it seem curious that the effect should not transfer under inducing conditions where one eye only was exposed to the coloured gratings. Transfer was looked for under a variety of conditions which ensured that the eye which was not exposed to gratings was nevertheless in use during induction and testing, and also that the input was not suppressed during induction (cf Baker, Mash and May, 1976) (Expt 6.21.2-3).

When this still proved unproductive of transfer, the problem was approached, as it were, from the other end. In a series of runs beginning with binocular exposure to a usual McCollough stimulus, the input to one eye was made progressively more dissimilar from the full McCollough stimulus simultaneously administered to the other, in hopes of pinning down the conditions which are essential for generation of an effect dichoptically (Expt 6 1.5)

3.3.3 A Binocular McCollough effect

Vidyasagar's elegant discovery in 1976 of a binocular element in the McCollough effect induceable by simultaneous use of the two eyes and visible only upon binocular testing, sent me back to our early finding (unpublished) that after ordinary binocular induction the effect measured binocularly was slightly larger than that measured in either eye separately. Various binocular exposure regimes were employed as controls, in all of which the two eyes were not exposed simultaneously to the same stimuli (Expt 6.3.1). All yielded binocular aftereffects which were smaller than the monocularly measured effects which were simultaneously generated by these same stimuli.

3.4 What are the essential aspects of the stimulus?

Throughout this work I have been interested by the question as to the minimal essentials for induction and for testing a McCollough-type aftereffect, for this will be a clue to the complexity of the mechanism which is responsible for the effect. McCollough's original inducing pattern had involved both orientation and pattern-spacing. Could they each serve separately as the feature upon which a chromatic aftereffect is contingent - orientation without a repetitive pattern? Spacing devoid of orientations? (Expt 7.1 and 7.2).

Was a real intensity edge necessary at the primary receptors, or could kinetic contours generate an aftereffect (Expt 7.3). Was a real extended edge necessary or could a rapidly moving dot serve as a 'stripe'?

Were real colours essential or could an effect be induced using subjective colours produced by a coloured surround?

The answers to such questions yield clues as to the level of sophistication in the visual system at which the McCollough effect occurs.

3.5 Essential features of the McCollough aftereffect

3.5.1 An opponent-colour "orthogonal inhibition"?

The notion that the human visual system might contain opponent colour linkages between systems signalling mutually perpendicular orientations

(ch 2.4.7) seemed so interesting and important as to merit closer scrutiny. In particular some control experiments were called for to establish Hajos's (1970) claim that a red grating produces a pink after effect upon a test grating perpendicular to itself. In the event several different approaches (Expt 8.1) yielded no sign of this orthogonal chromatic aftereffect and control experiments revealed less exciting explanations for the various phenomena which had been ascribed to interaction between systems handling mutually orthogonal orientations (MacKay and MacKay 1977b).

3.5.2 Angular sensitivity in the McCollough effect?

A question still, however, remained as to whether, when the McCollough stimulus consisted of two gratings at different orientations and alternately viewed, there was any interaction between the aftereffects which they generated. There are many achromatic demonstrations that straight lines affect perception in their neighbourhood both during and after their presentation (e.g. the Zöllner, Hering, and Poggendorf illusions; Fraser's twisted cord illusion ; Köhler and Wallach, 1944, fig 53; the direct and indirect tilt effects, Gibson and Radner, 1937; MacKay, 1957; Gilinsky, 1968). So it seemed quite possible that the McCollough effect would contain an angle sensitive ingredient.

It was indeed reported that chromatic aftereffects had been induced whose contingency was upon the concavity/convexity of mildly curved or bent gratings (Riggs, 1973; White and Riggs, 1974 resp). In these experiments the whole curve or angle was visible at once and fell (on average) upon different parts of the retina so the situation is slightly different from that in which the two gratings are sequentially presented to which we shall return in the next paragraph. Riggs and White did not control for those ordinary McCollough effects (of viewing straight coloured gratings) which their stimuli would undoubtedly generate. These aftereffects, corresponding as they on average must, to slightly different orientations on either side of the axis of symmetry of their patterns, would be expected to lead to chromatic aftereffects on curved and angled test patterns even though no curvature or angle sensitive neural machinery existed. Control tests in which similar curves (MacKay and MacKay, 1974, Expt 8.2, and Stromeyer in Stromeyer and Riggs, 1974) and chevrons (Sigel and Nachmias, (1975) were moved to and fro on the retina to equalise exposure to all parts of the inducing pattern, yielded no detectable aftereffects. This result suggests that if there are curvature or angle sensitive chromatic aftereffects they are very much weaker than the McCollough effect simpliciter.

3.5.3. The repulsion of the chromatic maxima

Nevertheless, there still remained a phenomenon in connection with the alternately presented straight gratings which had the appearance of an angle-sensitive chromatic effect. In studying the chromatic aftereffects generated by McCollough-style exposures to two gratings at a small angle (11°-30°) to each other, it was observed (Expt 8.2,1) that the strongest hues were not seen on the test figures when they were set at the orientations previously occupied by the inducing gratings, but at orientations "repelled" a few (c 15°) degrees further apart (Stromeyer in Stromeyer and Riggs, 1974; MacKay and MacKay, 1977). Riggs (1973), and White and Riggs (1974), observed what I take to be the same phenomenon in connection with both curves and chevrons; "Inspection of nearly flat angles or curves or cusps yields greatest strength of CAE's on test angles near 90°" (White and Riggs, 1974). This they took as clinching proof that

"There are cortical units that receive inputs from more than one set of line orientation units" (Riggs 1974) since "this finding would not be expected solely on the basis of line orientation specificity" (White and Riggs, 1974). But 'repulsion of the maxima' operating within each half retina must be considered as an alternative explanation to interaction between the systems signalling the two limbs of each curve or chevron.

To find, - in the case of straight McCollough gratings alternately presented at a small angle to each other - whether it is necessary to invoke angle-sensitive mechanisms to account for the repulsion of the maxima, I have compared the observed aftereffect distributions with those predicted by simple summation of the aftereffects generated by a red and a green grating (Expt 8.2).

Chapters 5-8 contain experimental explorations of most of the above questions. Within each chapter there is a largely historical sequence of experiments, but the four chapters may be read in any order.

CHAPTER 4 APPARATUS AND EXPERIMENTAL PROCEDURE*

There are always two stages to an experiment on McCollough-type effects; exposure to a visual stimulus, and observation of the resulting visual aftereffects. Generally (though not in Expt. 8.1, see below 4.1.4) I have used separate apparatus for these two stages of the experiment based upon slides and transparencies for projecting the inducing stimuli and (largely achromatic) paper figures for testing the aftereffects. This apparatus will be described and discussed part by part in sections 4.1 and 4.2. The complete measuring apparatus is described in 4.2.1, the conduct of the experiment in 4.3.

4.1 The stimuli used to induce chromatic aftereffects

The inducing stimuli were high contrast patterns presented through various colours of filter to one or both eyes.

4.1.1 The patterns

The patterns used were straight or curved (fig.41) square wave gratings, regular hexagonal arrays of circular dots at two magnifications and of both polarities of contrast, random dots (of the same size and average density as in the regular arrays), and random visual 'noise'. The spatial frequency of the gratings used ranged from 1.7 to 3.4 cycles/degree, and of the large and small dots was 1.8 to 4.6 dots per degree. The visual noise was a photograph of Zoll Raster: pattern no. 303 at magnifications differing by a factor of four. The test figures corresponding to these stimuli are shown in fig.2 , chapter 4.2 and fig.42 of chapter 8.3.

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* The reader may wish to skip this chapter and to refer back to it as necessary.

4.1.1.1 The use of oblique gratings

For most of the experiments on the McCollough effect I have used oblique gratings at +45° and -45° to the vertical. These were chosen in preference to the horizontal and vertical used by most other observers for the following three reasons:

4.1.1.1.1 The human visual system is known to have special sensitivities for orientation near the vertical and horizontal. These properties are not essential to the McCollough effect and are not identical for horizontal and vertical (e.g. Campbell, Kulikowski and Levinson, 1966; Hirsch, Schneider and Vitiello, 1974). The use of oblique gratings separated the McCollough effect from visual properties peculiar to the vertical and horizontal, and provided two orientations which are rather more symmetrical with respect to each other.

There is a considerably lowered angular acuity and threshold sensitivity at the oblique orientations, but for my experiments this loss did not matter as the McCollough effect is not sharply tuned for orientation, and patterns well above threshold were used throughout.

4.1.1.1.2 Secondly, the man-made world around us contains more high-contrast vertical and horizontal coloured edges than oblique ones. These will induce small but not negligible McCollough effects even before a subject commences an experiment (cf. Stanley and Hoffman, 1976) and during decay. These will lead to undesirable bias and scatter in the results. The use of oblique gratings, while not totally avoiding such influences diminishes them as much as is possible without withdrawing the subject from a normal environment between readings.

4.1.1.1.3 Lastly, it is much harder for a subject to remember which way gratings of a particular colour were oriented when they are oblique than when they are vertical and horizontal, and so correspondingly more difficult for subjects to work out what they think they 'ought' to be seeing.

4.1.1.2 The spatial frequencies of the patterns used

Gratings of from 1.7-3.4 cycles/degree and hexagonal arrays of spots of 1.8-4.6 cycles/degree were used. For some experiments a factor of two difference in magnification was deliberately chosen (e.g. 7.1 , 8.1.4). It will be remarked that the patterns used were not the finest that might have been chosen. Grating frequencies of around 5 cycles/degree have been found (chapter 1.6) to give strongest McCollough effects. It was, however, found that fine gratings were more tiring for the subject in testing. This was perhaps because small eye movements were more disturbing than on a less fine pattern.

4.1.2 Colour Filters

The colour filters used in every experiment to be described here were Cinemoid 'ruby' and 'dark green' (14 and 24 resp.). These are fairly narrow bandpass filters (590-670 nm, 480-560 nm resp.), which are moderately good colour complements. When light which has passed through them is mixed, a yellowish-white light is produced.

To match the luminances transmitted in these two colours, one layer of the red, and two of green filter were used with 100 watt projector bulbs, and two layers of red and three of green with 500 watt bulbs and the Daylight (6 watt 54 VL) tubes of the tachistoscopes.

The colour filters were attached, as was convenient, in front of the lenses of the projectors, or to the transparencies (in the Boots auto projector, E_3 and the tachistoscopes E_4, E_5) or held close by the subject's eyes on a mechanical arm or in the subject's own hand and moved during the dark periods synchronously with the shutter which changed the image on the screen (E_1, two projectors).

Because of their near monochromacy these filters were preferred to the Wratten magenta and green filters (34A and 53 resp.) which have been used in many experiments on the McCollough effect by other workers. For though the Wratten filters are exact colour complements and produce a slightly larger McCollough aftereffect, they are both band stop filters. As the magenta filter transmits considerably in the blue, the extent to which the blue receptors are involved is rendered unnecessarily uncertain by its use.

4.1.3 The timing of the presentation cycle

In every experiment (except 8.1.4) two stimuli, patterned or, occasionally, unpatterned, were presented alternately for equal lengths of time with dark periods between. In the timing cycle most frequently used the stimuli were presented for 6 seconds apiece and the intervening dark periods each lasted 3 seconds. Other timing cycles ranging from 15 sec ON/3 sec OFF to ½ sec ON/½ sec OFF and 9 sec ON/9sec OFF were occasionally used. In one experiment (6.1.4), in order to replicate the conditions employed by another group, ON periods of 120 msec were used.

4.1.4 Apparatus for presenting the stimuli

In every experiment (except the two on kinetic contours and persistence of vision) a projector, a pair of projectors, or a tachistoscope were used for presenting the inducing stimuli. Presentation was always in a darkened room to maximise pattern contrast.

The particular requirements of the various experiments determined the choice of projector or tachistoscope. Six different arrangements were used which will be referred to in the text as E_1-E_6.

McCollough exposure apparatus

E_1: Two projectors with shutter

For the experiments (5.1, 5.8, 6.1, 7.2) in which two stimuli were to be presented alternately, in good focus and at constant orientations, two small projectors holding the two slides were set side by side upon a shelf above the subject's head, and a shutter was moved electrically to and fro to cover the lens of one or both of them. An electronic timer controlled the on/off cycle provided by the shutter. Both on and off periods could range from about ½sec to 15sec. The main requirement for the two projectors was that they should be slim so that the images they produced should not be badly distorted when the two projectors were directed towards the same part of a screen at 100 cm. Two Jugoslavian 'Plusjector 150A' with 100 Watt bulbs (sold by Boots) were set with their axes 10 cm apart. For the dichoptic experiments (Experiment 6.1.1) the projectors had to satisfy the further requirement that there should be no colour difference between the achromatic images which they produced. Heat absorbers and lenses were selected to make up two identical projectors, and by moving the shutter by hand in front of the two projectors at about 2-3 Hz it was possible to check fairly sensitively that the images were matched in colour. A check was made that no significant McCollough effect was seen after 20 min exposure to the two achromatic slides alone and runs on the dichoptic effect were always performed in pairs with which the pairing of colour and orientation reversed in the two runs.

The subject used a chin rest to view the patterned stimuli from 105 cm. The subtense at the subject's eye of the gratings used in Experiment 5.1. and Experiment 6.1 was 2.5 cycles/degree, and of the spots used in Experiment 7.1 was 1.8 and 4.6 cycles/degree. The patterned fields subtended $17^{\circ} \times 11^{\circ}$. The luminances of the red green and white areas of the patterns were 3.5, 3.9 and 8mlm respectively, and the black areas were 20 times dimmer.

E_2: Braun projector

In some experiments a large field was required with no distortion and an accurately known spatial frequency (Experiments 5.4.4.1, 7.1). For these a Braun projector (500 Watt) was used at 2-5 m from a 6 ft Westone plain screen and the subject sat close (2.8 m) to the screen. The subject generally held the colour filters in a frame in his hand because a) the projector objected to bulky slides and b) different colour pairings were often presented to the two eyes simultaneously. A presentation cycle of 9 sec on 1 sec off was employed.

The subtense at the subject's eye of the gratings used in Expt 5.4.4.1 was 1.3 cycles/degree and of the small and large spots in Experiment 7.1 was 4·6 and 1·8 cycles/degree respectively. The pattern subtense was about 70° in each case. This was the only apparatus with which the subject's state of accommodation was widely different during exposure and testing, the viewing distances being 2.8 m and 68 cm respectively. The luminances of the red green and black areas of the patterns were 6.8, 6.0 and 0.3 mlm respectively.

E_3: Boots autofocus projector

For experiment 8.1 in which a set of up to 8 grating slides were to be presented repeatedly and at precise angles, the 'Boots Autofocus' (with 150 Watt bulb) was chosen because it has a V-shaped horizontal groove along which the slides are gently pushed into position by a horizontal arm. The orientation of the gratings was repeatable to better than ½°. This projector also had a convenient automatic slide changer with a built in timer, so the subject had only to press the 'reverse' button each time the last slide in the magazine was reached. A presentation cycle of 7 sec on/ 1 sec off was employed. To minimise image distortion the subject's bite bar was set as close as possible to the axis of the projector and the Bristol board screen was tilted a little towards the subject from the normal to the projector's beam. The stimuli were red/black or green/black gratings subtending 2.2 cycles/degree, luminance 8 mlm and 2 log units contrast, or else unpatterned red or green fields of 4 mlm.

E_4: A four field tachistoscope

A four field tachistoscope which gave on times of up to ½ sec was used for dichoptic experiments with split fields (Experiment 6.1.7.1). Presentation cycles of ½ sec on 0 sec off were used. Rear illumination of the stimuli was provided by 'daylight' tubes. Slight differences in the blueness of the light reflected from the half silvered mirrors were corrected by the insertion of pale blue filters in front of these tubes. The luminance of the white stripes of the gratings was 2.4 mlm and of the unpatterned coloured fields was 0.4 mlm. When the subject was using the chin rest at 56 cm the fields subtended $15^{\circ} \times 15^{\circ}$ at his eye and the gratings used subtended 1.9 cycles/degree.

E_5: A four field tachistoscope

A four field tachistoscope capable of giving long presentation cycles was built by Keith Bradshaw and used for some binocular experiments (6.1, 6.3). A presentation cycle of 9 sec on 9 sec off was employed. The mirrors of this tachistoscope introduced no noticeable hue differences. The rear illumination of the stimuli was provided by daylight tubes. The luminance of the red and green stripes was 5 and 6 mlm and the black stripes were 20 times dimmer. When the subject was using the chin rest the fields subtended $15^{\circ} \times 25^{\circ}$ at his eye and the gratings used, 3.2 cycles/degree.

E_6

In experiments 8.1.4, 8.1.5 the measuring apparatus M3 was used to present the inducing stimuli in order that the orientation and spacing of the patterns and the position of the subject's head (fixed by a bite bar) should be identical during induction and testing. The two projectors of M3 were so aligned before the experiment that, when they projected identical slides, the images they cast in the two concentric parts of the subject's field of view formed a single grating. The colour mixer was set to match the neutral surround. The subject placed hand-held red and green filters between his eye and the Dove prism, moving them (in Expt 8.1.5) so that as the slides in the ganged projectors automatically alternated every 8 sec, a grating of a particular spatial frequency was always seen through a particular filter during a given run. In Expt 8.1.4 a single spatial frequency of slides was presented continuously and the green or red filter was fixed to the eye ring. The luminance of the gratings was 1.9 mlm and the contrast one log unit. The angular subtense of the field was $19^{\circ} \times 20^{\circ}$, the mask which limited the test field to 15° having been removed for the inducing exposure. The gratings used subtended 1.7 and 3.4 cycles/degree at the subject's eye.

4.1.5 Monocular, binocular and dichoptic exposures

The stimuli presented to the two eyes were made to differ in systematic respects in order to elucidate the extent to which the two eyes interact in orientation-contingent aftereffects.

4.1.5.1 To expose a subject monocularly, the unexposed eye was covered by a black eye patch on an elastic or–(this was more light tight)- by the subject's cupped hand. For some experiments a completely light tight arrangement of padded goggles, masking tape and foam rubber across the bridge of the nose was used. Even with this, once the occluded eye had dark adapted, a dull red glow was visible on the side nearest the nose when light entered the other eye. But this glow did not noticeably change its appearance when the light in the other eye changed colour.

4.1.5.2 For binocular exposures projectors (E_1 or E_2) or a tachistoscope (E_5) were used. The tachistoscope could present stripes at orientations which were the same or different for the two eyes in the same or different colours, on timing cycles which were in or out of phase for the two eyes. When the projectors were used both eyes viewed identical patterns on the screen through colour filters (and/or neutral density filters) which were the same or different for the two eyes. These filters were arranged in a double-decker lorgnette suspended from a horizontal arm. In E_1 this arm was operated by the same current which moved the shutter in front of the two projectors but with the Braun projector, E_2, it was moved by the subject at the time that he operated the slide change button. In each case the filters moved during the dark part of the presentation cycle.

4.1.5.3 For dichoptic induction tachistoscopes (E_4 and E_5) were used for the later experiments in which split fields and various other complicated combinations of pattern and colour were presented to the two eyes (see Expt 6.1.4 , 6.1.6.1). For many experiments (MacKay and MacKay, 1973, 1975 and Experiment 6.1.1 .) two projectors with a shutter (E_1) were used to present pattern to one eye while a small lamp illuminated unpatterned coloured fields at the other eye. There was one prime consideration in the latter experiments; that each eye should not see the stimuli intended for the other, or any reflection or systematic accidental feature of such a kind as to produce a monocular McCollough effect.

The arrangement used in Expt. 6.1.1 ,(MacKay and MacKay, 1975) consisted of two matched projectors (E_1) (see 4.1.4) for presenting the patterns, and a 12 volt car head lamp or a two volt pea lamp in a light-tight housing close against the subject's eye. The lamp was covered by several layers of fine tissue paper 3 cm in diameter and red and green filters were supported between these and the subject's eye. The resulting coloured field was fairly uniform and sufficiently wide (30^{c}) that no edges or borders fell within the (15^{o}) area to be tested later for a McCollough effect. A black card at 30 cm from this eye completely cut off the view of the projection screen and also removed any possibility that coloured light cast onto the subject's face could reflect back onto the projection screen. A very dim reddish glow shone through the bones of the nose to the 'patterns' eye, but it fell well to the nasal edge of the field and did not change colour when the colour filter was changed from red to green.

The patterned and coloured stimuli were presented to the two eyes simultaneously for 6 sec on periods separated by 3 sec of darkness. The orientations of pattern and the colours of the plain fields were alternated, each orientation being paired with a particular colour throughout a particular exposure. An electronic timer controlled the presentation of the stimuli by determining the current to the head lamp or pea lamp at the subject's eye and the positions both of the colour filters and of the shutter in front of the two projectors (E_1).

4.2 Apparatus for observation and measurement of the aftereffects

Measurement was used as a check upon simple observation and verbal report in almost every experiment to be described. All the qualitative effects to be reported can in fact be readily observed with no apparatus beyond an appropriately patterned paper test card held in the hand,* but the variants on a colour matching device used throughout these experiments were invaluable in enabling the experimenter to distinguish definite from insignificant results and in relieving the subject of the need to make frequent verbal judgements. The apparatus was thus as useful in those experiments - and they form the majority - which are essentially qualitative as in those which deal with the forms of the time courses.

4.2.1 Apparatus for measuring the McCollough aftereffects by hue matching and hue cancellation

Three variants, M_1, M_2, M_3 (figure 1a, c, d) on the hue measuring device are outlined in this section, their details are described and discussed in sections 4.2.2-4.2.5. The mode of conducting the experiment is described and discussed in 4.3, 4.4.

Test apparatus M_1 (figure 1a) gave a binocular or monocular view of a 15° test card of the 'two half' type (figure 2, T_2-T_7), front illuminated by a Cryselco 'Warm White' 32 watt ring tube. A shutter, close to the subject's face, could occlude either eye or neither. A smooth knob under the subject's control varied the hue and saturation of the light from the colour mixer rear illuminating the two translucent windows in

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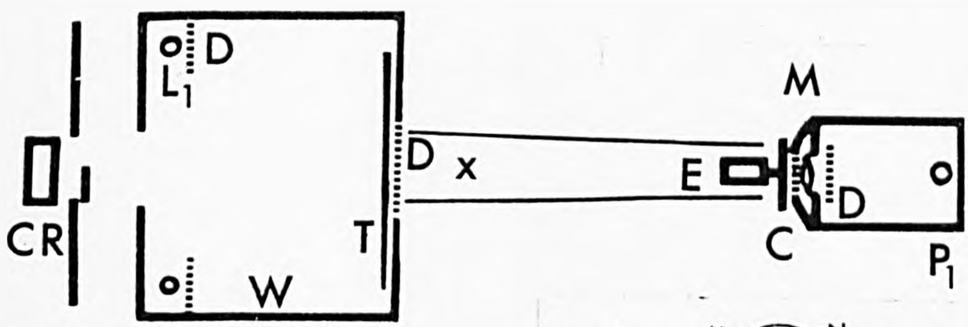
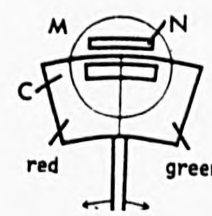
* None of the experimental data which follow were collected in so informal a way because luminance, angle and viewing distance affect the observed strength of the aftereffect.

fig I: Apparatus for Measuring Pattern-Contingent Chromatic After-Effects

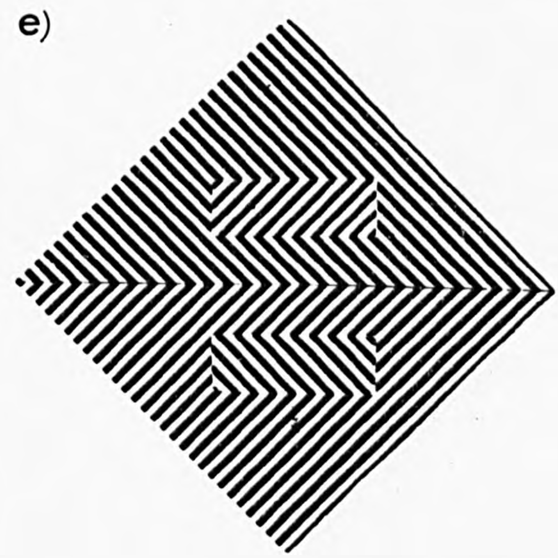
a) Version M_1



b)

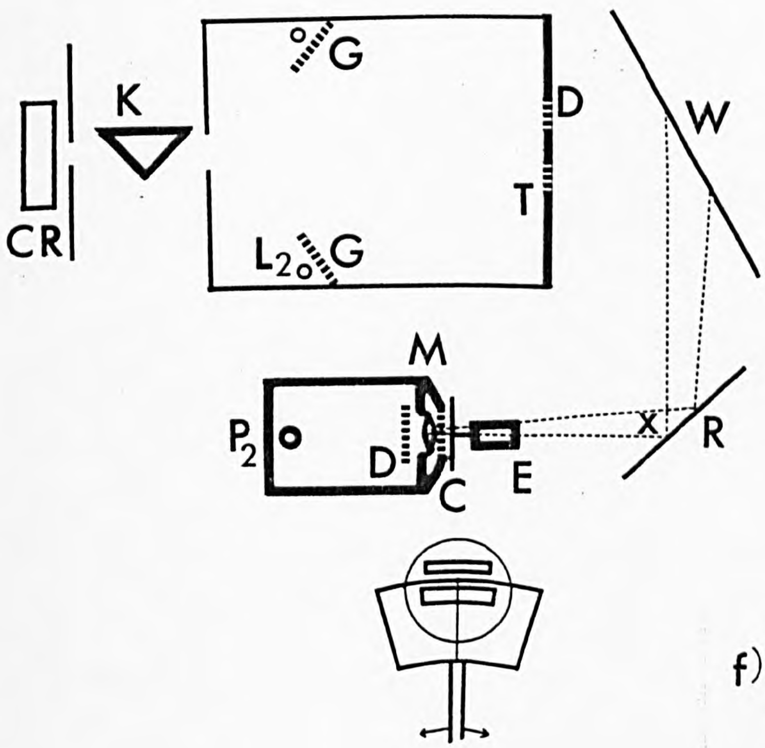


e)

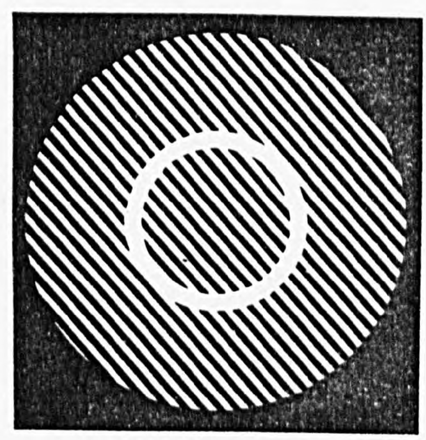


(a), (c), (d) Three versions M_1, M_2, M_3 of the hue measuring apparatus,
(b) detail of the colour filter as seen from X,
(e) one of the test figures used with apparatus M_1 (fig. 2 shows further test figures),
(f) test figure used with apparatus M_2 (the rear illuminated annulus has outer diameter 7^o width 0.7^o),
(g), (h) the two test figures seen sequentially by the subject in apparatus M_3 (the diameters of the outer and inner circles were 15^o and 5^o).

c) M_2

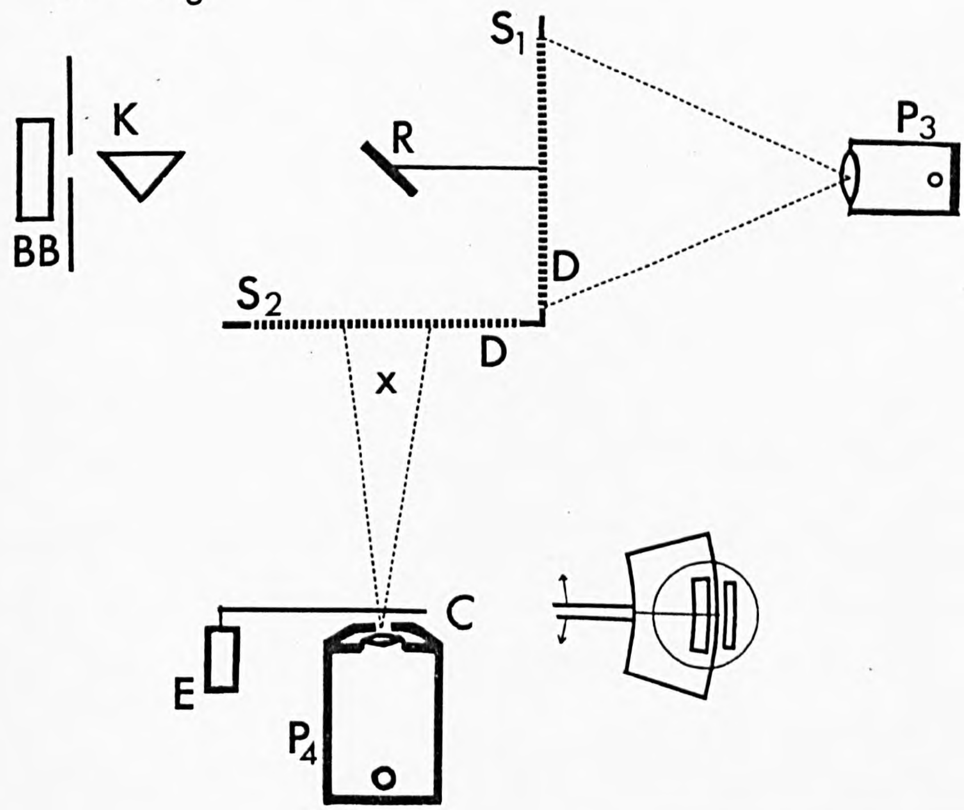


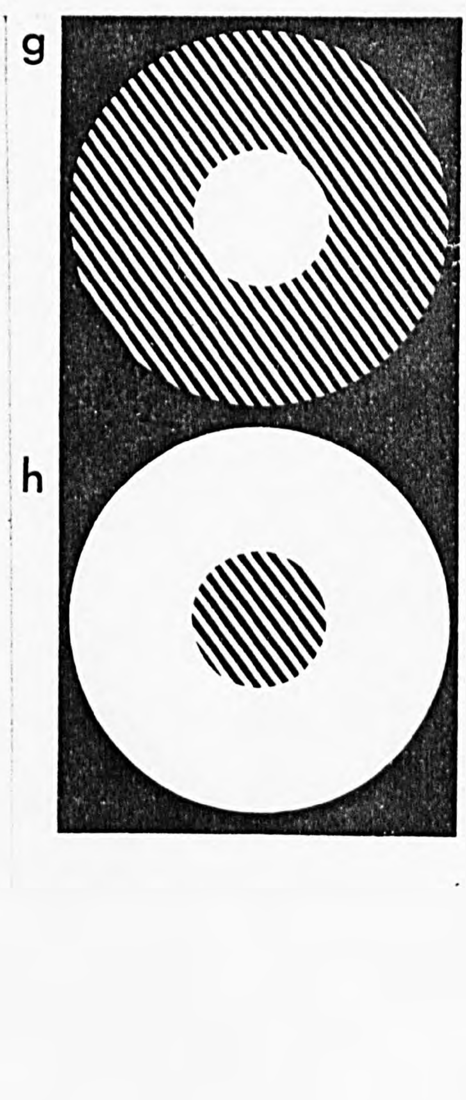
f)



BB, bite bar; C, movable red and green (or pink and pale green) filters; CR, chin rest; D, translucent tissue; E, pen motor; G, opal glass; K, dove prism; L_1, ring lamp; L_2, pea lamps; M, mask over lens of projector P_1, P_2, P_4, central aperture 1.1 x 3.3 cm; aperture N 0.5 x 3.2 cm; N, aperture in mask M admitting white light; P_1, P_2, P_3, P_4, projectors (tungsten filaments); R, mirror (front silvered); S_1, S_2, back-projection screens; T, test figure; W, white diffusing card.

d) M_3





the test card. The position of the movable colour filters in front of the projector P_1 (and thus the ratio of the excess* of red over green light to the total light falling on the 'windows') was recorded as a function of time by an X-Y plotter. The difference S cm between the subject's hue match settings for the upper and lower half fields was taken as a measure of his McCollough effect at that time.

The test apparatus M_2 (figure 1c) had a monocular eye ring and a rotatable Dove prism through which there was a view of a 15° test field (T_1), front illuminated by two pea lamps. A smooth knob under the subject's control varied the hue and saturation of the light from the colour mixer which was rear illuminating the translucent annulus of the test card. The position of the moveable colour filters in front of the projector P_1 (and thus the ratio of the excess of red over green light to the total light falling on the annulus) was recorded as a function of the Dove prism's orientation by an X-Y plotter. The difference between the subject's pre- and post-exposure hue matches at a given orientation was taken as a measure of his post-exposure McCollough effect at that orientation at the time of the post-exposure measurements.

The test apparatus M_3 (figure 1d) had a bite bar, a monocular eye ring and a rotatable Dove prism through which there was a view of the 15° test figures T_9 and T_{10} (or T_{11} and T_{12}) which were presented alternately. These were produced by back projection on the tissue screens S_1, S_2 of slides in the two projectors P_1 and P_2. A smooth knob under the subject's control varied the hue of the light from this projector. The position of the moveable colour filters in front of the projector P_1 (and thus

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* 4.2.3 gives details; also 5.1.1.

of the ratio of the excess of pink over green light to the total light falling on the mirror) was recorded as a function of the Dove prism's orientation by an X-Y plotter. The difference between the subject's hue match settings for the two test fields (i.e. between a hue match and a hue cancellation at a given angle) was taken as a measure of his McCollough effect at that angle.

An on-line C.A.I. alpha computer was used with M_3 to control the position of the Dove prism and the changing of the projector slides, and also to record the subject's settings. To turn the Dove prism to various pre-selected orientations in random order the computer signalled to a Crouzet (type 82752) pecking motor which was connected by a chain drive to the rotatable prism housing. The prism remained at each position while two match settings were recorded, one for each of the two pattern arrangements (T_9 and T_{10}) that were provided by the projectors.

4.2.2 The test stimuli

The aftereffects were observed either on cards bearing black and white high contrast square wave gratings ('Plastitone' SH4) or on photographic prints, or on tissue screens upon which the patterns were back projected from '2 x 2' slides.(apparatus M_3). The angular subtense of the patterning was in each case matched to that of the inducing patterns at between 1.7 and 3.4 cycles/degree for the gratings and 1.8 to 4.6 repeats per degree for the dot patterns.

4.2.2.1 The test figures

All the test fields used (with the exception of the kinetic contours of experiment 7.3) are shown in figure 2 and in figure 42 of chapter 8.3.2. Those of figure 2 when viewed at 65-95 cm subtended 15° to 12°, those of figure 42 a and b, $7.2^\circ \times 5.4^\circ$ and $6.3^\circ \times 9.0^\circ$ respectively.

fig 2

TEST FIGURES

for measuring pattern-contingent chromatic a-e's

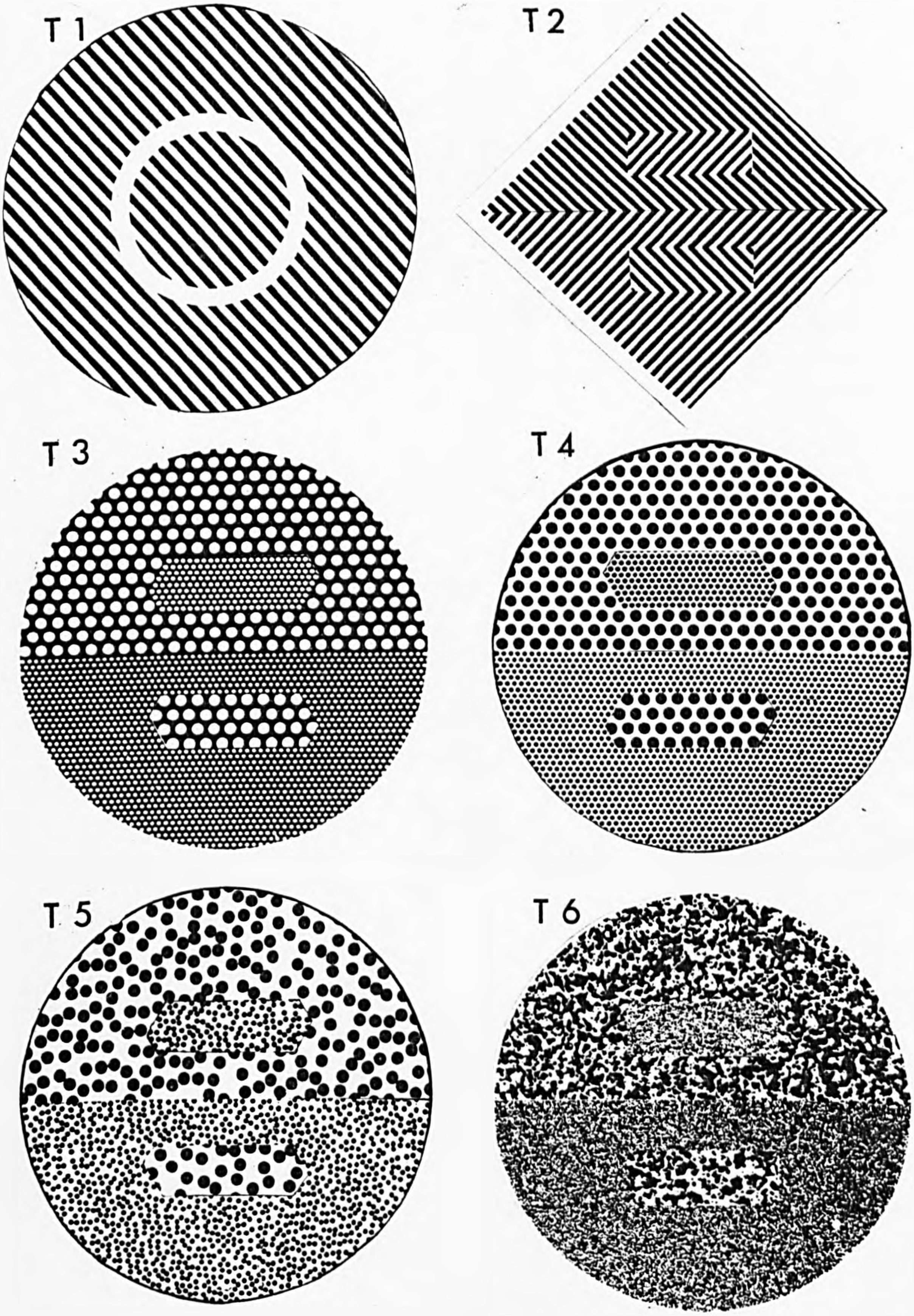
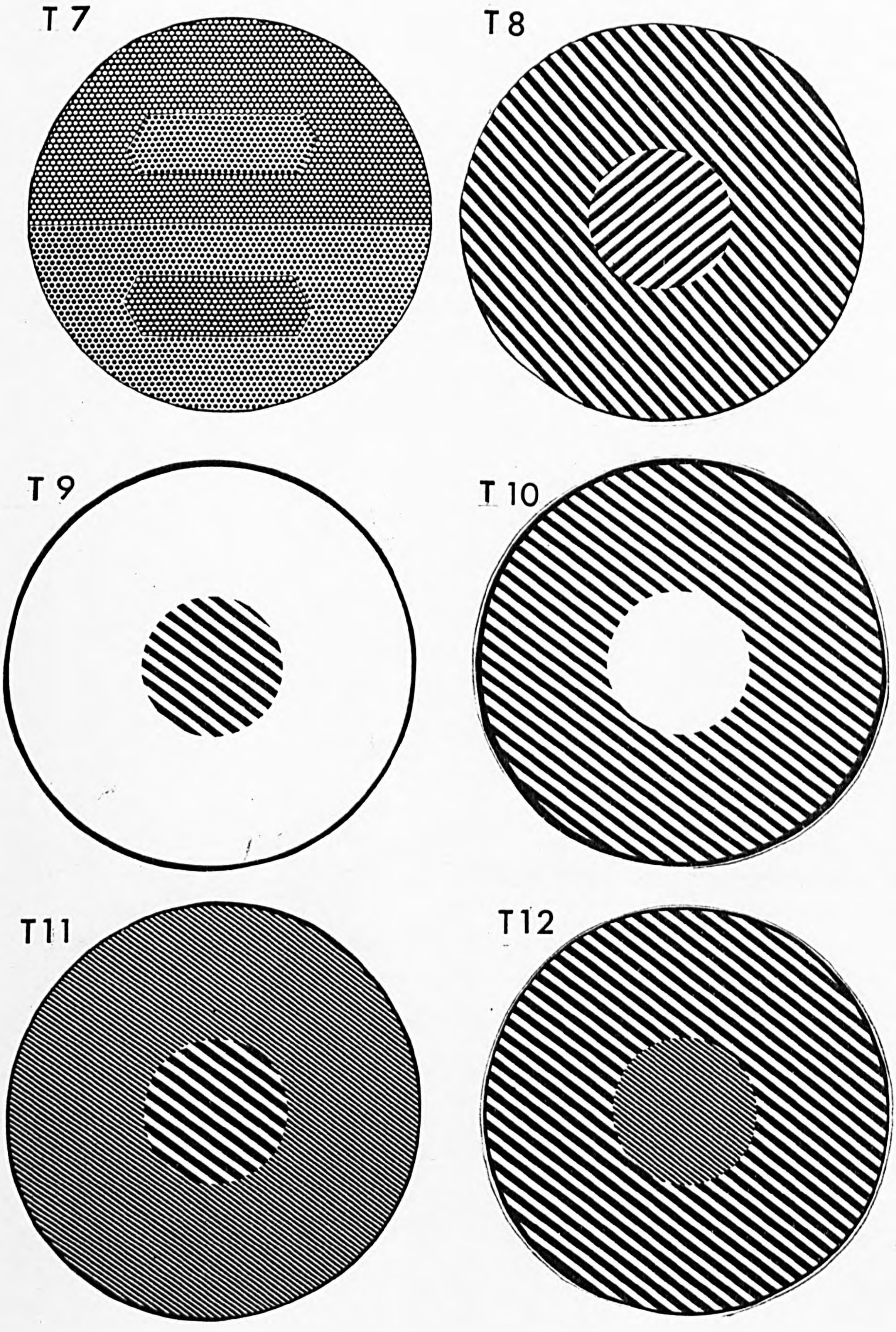


fig 2 (cont)



Each had a frame of black card and was seen in the test apparatus within the black field provided by masks or eye rings nearer the subject.

Each test field contained two differently patterned areas, one of which might be plain, so that the comparisons of the hues seen on the two parts could be made. Comparisons are much to be preferred to attempts at 'absolute' judgements (in which no steady reference is provided), since they are not subject to 'D.C.' drift of the subject's internal hue criteria. The McCollough effect hues are more prone than real colours to such drift when simultaneous and successive colour contrast is present (cf. experiment 8.1.2).

The three, slightly different, forms of test field used with apparatus M_1, M_2 and M_3 are typified by T_2, T_1 and the pair T_9 and T_{10}. In each the colour of the central area was variable by the subject.

4.2.2.1.1 The first type, T_2-T_7, had two symmetrical half fields in each of which was a translucent 'window' measuring $5^o \times 2^o$ and filled by 'plastitone' grating or kodalith prints whose patterning matched that of the other half field. These windows were closely backed by a uniform tissue paper (Chartwell tracing paper).

Figure 2 Test figures

Approximate representations of the principal test figures used to observe and measure pattern-contingent chromatic aftereffects. All were viewed from such a distance (65-97 cm) as to subtend about 15^o. The gratings of T_1, T_2 and T_8 subtended 2.0, 2.2, 1.7 cycles/degree respectively. The patterns of T_3, T_4 and T_5, 1.8 and 4.6 dots/degree and those of T_7 3.1 dots/degree.

4.2.2.1.2 The test card T_1 (for use with apparatus M_2) had a translucent 'window' in the form of an annular ring of diameter 5.7° and width 0.6° (at 65 cm). This arrangement allowed the fovea to be occupied by pattern, yet provided a sizeable tinted area and a long boundary at which to perform hue matching.

4.2.2.1.3 In test apparatus M_3 (cf. T_9 and T_{10}) the test field had two concentric areas of diameter 15° and 5° (at 56 cm), whose patterning was provided by images of slides thrown by two projectors.

4.2.2.2 Patterned central areas or 'windows' were used, whenever the type of experiment allowed, for the following reasons:

4.2.2.2.1 It made it possible for both the mean luminance of the whole window and the local luminance of the bright areas of the window to be made identical with those of the surrounding test area. Luminance differences make hue matching difficult.

4.2.2.2.2 Unpatterned areas are more difficult to work with than patterned ones. They take on a 'blotchy' appearance and sometimes seem 'dazzling', sometimes 'bleached'. From measurements made using versions of T_2 (figure 2) with and without patterned windows, it was found that the standard deviation was slightly larger when plain windows were used.

4.2.2.2.3 The quantity S being measured is increased (by about 30%) because hue cancellation is added to hue matching.

The accuracy of the results is thus improved by using patterned windows, both by the decrease of standard deviation and by the increase in the quantity measured.

4.2.3 The colour mixer

The central, differently patterned, regions of each of the above test cards were illuminated by the colour mixer. In each version of the apparatus the principle of the colour mixer remained unchanged.

As close as possible in front of the lens of a low powered projector, P_1 (100 watt in M_1, M_2, 8 watt in M_3) a movable colour filter (figure 1b) was supported by an aluminium arm fixed to the axis of the EEG pen motor E. The filter consisted in M_1 and M_2 of red and green filters and in M_3 of pink and pale green filters,* abutting in a straight line passing through the axis of the pen motor. The pen motor current was thus linearly related to the displacement of the colour filter.

The projector lens was fitted with a mask having two slits of 4.6 cm x 0.5 cm and 4 cm x 1.1 cm whose long axes ran in the direction of motion of the colour filter. The lower, curved** slit admitted light to the colour filters, the upper slit added white light which diluted the coloured light to a suitable range of saturations for matching McCollough hues.(fig 1b)

With the dimensions above and the approximately monochromatic filters used in M_1, M_2, the maximum saturation is 15% ± 2%. This

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* The red and green filters used with M_1, M_2 were 1 layer of red and 2 of dark green (cinemoid 14 and 24). With these the aperture N was open. The pink and green filters used for figure 37 of experiment 8.1.4 were:
Figures 37 a, c Pink: Cinemoid 54 'pale rose' (1 layer); Green: Pilkington's 3/16" 'antisun' glass; aperture N closed. Figure 37 b Pink: Cinemoid 54 (2 layers); Green: Cinemoid 38 'pale green' and 67 'steel tint' (one layer of each); aperture N open.

** The radius describing the curved slit had its centre at the axis of the pen motor.

corresponds to a reading of S = 4.2 cm on the scale used for the figures of chapters 5-7. The scale used in chapter 8 is about 10 times larger (a subject's fairly steady McCollough effect was used as the means of cross calibrating M_3 with M_1).

If the light passing through the curved slit in the mask is uniform* in intensity, the pen motor current, i, is linearly related to the excess of red over green or vice-versa in the total light in the colour mixture. (The colour filters having been so chosen that this total - the denominator below - was near constant.)

That is, $i \propto \dfrac{L_R - L_G}{L_R + L_G + L_W}$, where L_R, L_G, L_W are the luminances contributed by the red, green and white sources respectively.

4.2.3.1 <u>Obtaining a uniformly coloured field from the colour mixer</u>

Mixing of the two coloured parts and the white part of the projector beam was found to be best achieved by placing the moveable colour filters as close as possible to the projector lens. (Where necessary the lens hood was sawn off.)

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* In practice the W shaped filaments of the Atlas 1A lamps used in M_1 and M_2 gave a rather non uniform distribution of intensity along the length of the slit. Uniformity was much improved by defocussing the lens, and by placing diffusing tissue in the slide carrier and in the mask in front of the lens.

In M_3, such measures could not be adopted since a sharp image of a grating slide was to be produced by the variably tinted light. A 10 watt bulb with a uniform linear coiled filament (Lucas 12 v 265 'power-bulb') with its axis perpendicular to the dividing line in the movable colour filter proved a good solution.

The slight residual red/green gradient across the field at the test card was dealt with in slightly different ways in M_1 and M_2. In M_1 a reflecting horn of white paper 3/4 m long, greatly reduced the colour gradient. After June 1976 this was replaced by 2 sheets of tracing paper (37 x 25 cm) hung at one third and two-thirds of the distance (80 cm) from projector to test card. This arrangement gave an almost perfectly uniform field in the region which included the two 'windows' of the test field.

In M_2 a more compact scheme was used which gave equally good colour mixing; the projector beam fell (via a 45° mirror) onto a piece of white Bristol board at 20° to its path and 30 cm from the projector. This board was set 9 cm behind the test card and almost parallel to it.

In M_3 a smaller area of the tinted field was used (5 cm wide as against 10 cm in M_1 and M_2) and uniformity of saturation was quite good within this region with the unsaturated filters that were used.

4.2.4 <u>Illumination of the test card</u>:

The colour mixer illuminated a central area of the test field. The remainder was independently illuminated; in M_1 by a Cryselco ring tube; in M_2 by pea lamps; in M_3 by a projector (P_2) Suitable adjustments were made in each case to the lamp current, and to the surrounding reflecting surfaces and filters until the colour and luminance of the two regions of the test field matched when the colour mixer was at its neutral position.

The <u>luminance</u> of the test fields was 4 mlm in M_1, 0.45 mlm in M_2 and 3 mlm in M_3.

<u>Contrast</u> of the black and white areas of the test card was 2 log units in apparatus M_1 and M_2, 1 log unit in M_3.

Low luminances of the test card were chosen for the following three reasons:

4.2.4.1 because the McCollough aftereffect hues are more strongly visible (cf. Stromeyer, 1971).

4.2.4.2 because it was found that the McCollough effect decays less rapidly at lower luminances. (This consideration was of particular concern in the experiments of chapter 8 where it was desired that as little decay as possible should occur during the taking of some 60 readings at different orientations.)

4.2.4.3 to minimise the after images and alterations of sensitivity to colour and pattern that are produced by viewing the test card.

4.2.5 Recording the hue match settings and other variables

The variable from which a measure of the subject's McCollough aftereffect was obtained was the current, I, to the pen motor E of the colour mixer. This was recorded, in some experiments as a function of time (chapters 5, 6, 7) and in others as a function of the orientation of the test grating (chapter 8). Various pen recorders were used at different times to record the two variables - a Hewlett Packard 7035B X-Y recorder, a JJ chart recorder type CF100, and a Bryans plotter, each with suitable modifications and additions.*

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* Some of the modifications allowed various useful pieces of additional information to be automatically recorded. For example, a 5 Hz ripple, added to the signal, produced a line instead of a dot symbol (see figure 3). This could be used to record whether the subject pressed the recording switch away from, instead of towards himself (4.3); or (in M_1, M_3) to record which window or pattern configuration the subject was adjusting; and in M_2 to distinguish clockwise and anticlockwise traverses or earlier and later readings.

In M_1 the mean position of the plotter pen could take 3 values corresponding to the 3 possible positions of the shutter in front of the subject's eyes.

For the orientational studies the position of the Dove prism was recorded by means of a 10 KΩ linear potentiometer turned by a chain running on the toothed circular rim of the prism housing.

4.3 Conduct of the experiments

Ishihara-normal unpaid subjects were used. The subject was shown a test card (generally removed from its housing) and it was explained to him, without mention of aftereffects, that his task would be to match the hue of the differently patterned central area with that of its immediate surround. He was shown that by turning the colour mixer knob he could control the colour of the window and was encouraged to practise for a few minutes making hue matches. He was generally told, 'you will probably never feel the match is perfect. But if you turn the knob slightly one way you will be sure it is slightly too pink, if you turn it a little the other way it is too green. So home in rapidly, as in tuning a radio, and make a decision in the middle. There is nothing to be gained by being very slow and very careful; a number of quick and moderately careful measurements are much better than a few very slow ones'. Whilst practising the subject was accustomed to the test regime to be employed later. In the case of the two half test fields (T_2-T_7) he was asked to attend first to the upper half field and to match its 'window' to the surrounding triangular area while looking at the middle of the window and when satisfied to record his setting by pressing a switch in his right hand away from him. He then proceeded in a similar fashion to the lower half field, pressing the recording switch towards himself. In the apparatus M_3 the two test patterns were each presented at each chosen orientation, and the subject made the hues of the two areas match for each configuration. In M_2 one hue match setting was made at each orientation before the Dove prism rotated the view. When using M_3 the subject closed his eyes to rest while the test field was rotating.

When the subject was familiar with the apparatus he was asked to take a little rest (generally in darkness).

4.3.1 Pre-exposure testing was performed under the precise conditions which were to be employed in the post-exposure testing. Thus in the experiments on the angular distribution of the aftereffect, after spending 10 min in darkness, the subject performed a full set of up to 66 hue matches, the test grating being presented at the angles and in the sequence which was to be used in the post test. For the experiments using apparatus M_1, a group of 2-8 pairs of match settings on the upper and lower windows were performed as described in the previous paragraph.

Subjects whose bias was appreciable were asked to return at a later date, in the hope that the bias would fade. Biasses due to astigmatism did not fade.

Until June 1976 most measurements were made in a darkened room; after June 1976 the room was steadily lit (at 0.5 log ft L) so that the eye not being tested should receive light and be kept at a more steady state of adjustment (see 4.3.3 below).

4.3.2 The McCollough exposure

Upon completion of the pretest the room was darkened, the subject's chair was moved to face the screen or tachistoscope, the subject was settled on the chin rest or bite bar (if used) and exposure commenced some 10-50 sec after the end of the pretest. Subjects were asked to keep their heads upright and still. They were asked not to fixate but to keep the pattern in focus and to rove their eye around the patterns, preferably in small circles alternately clockwise and anticlockwise, for equal lengths of time. Generally the experimenter chatted with the subject about matters not connected with the experiment to ensure that the subject was not asleep. Shortly before the end of the exposure the subject was told what the next steps would be. To terminate the exposure he was given a signal to close his eyes. The duration of the exposure was timed using a stop watch, and in the temporal studies the beginning and end of the exposure were marked in the margin of the plotter paper.

4.3.3 Post-exposure testing

4.3.3.1 Runs using M_1 : the measurement of the decay course

For runs until June 1976 the subject, with eyes closed, was returned quickly to the test apparatus and when he was comfortable on the chin rest was asked to open his eyes and proceed immediately with hue match settings, in the darkened room as during the pre-test.

From June 1976 onwards the procedure was slightly altered. The subject was asked to close his eyes for about 10 sec and then, when the room lights had been turned on, to open them and view a large unpatterned white card (of 60° subtense and 0.5 log ft L) for a minute before proceeding to the hue match settings. The room lights were then left on. The shutter close to the subject's eye was covered by white paper and had a luminance of about $\bar{1}.7$ log ft L (higher luminances were found distracting). These modifications were introduced in order to standardise the conditions under which readings - particularly the early ones - were made. The time at which the eye was opened was taken as time origin in plotting most results (see 5.1.1).

When he had completed the first batch of hue matches the subject was often invited to describe in his own words any colour differences he saw between the two achromatic regions of the test field. If he reported none he was, in some cases (e.g. experiment 6.1), asked 'If you had to say that one of the two half fields was pinker or greener than the other, what would you say?'. Those still unable to report a difference were not pressed further.

Between batches of readings the subject engaged in normal life either outdoors and indoors, or in some runs only indoors at a constant luminance level of 1.1 or 0.5 log ft L. The policy of keeping the luminance level fairly steady both between and during measurements for both eyes noticeably reduced both the scatter within each group of readings and the scatter of the series of groups about a final curve. The intervals between batches of readings varied with the subject's convenience and ranged from 5 min to several hours.

4.3.3.2 For the studies of the angular distribution function hue match settings were made as described in 4.3, the view through the prism being turned to selected orientations, generally 11° apart or closer, either in random order three times over (M_3), or progressing systematically clockwise and then, after a ½ min rest, anticlockwise (M_2).

4.4.4 Accuracy, reliability, calibration

The reliability of the apparatus will be treated first and then that of the subject's measurements.

4.4.1 Accuracy in recording

4.4.1.1 The hue match settings

The linearity of the relation between the positions of the colour mixer filter and of the plotter pen was checked directly for each apparatus by placing a ruler against the colour filter. There were no signs of any non-linearity but there was about 2% hysteresis.This corresponds to 0.5 mm in M_1 and means that the accuracy of readings of the quantity S, ranges from better than 2% for single readings of strong aftereffects (S = 3.5 cm) to only 35% for barely perceptible aftereffects (S = 0.2 cm).

4.4.1.2 Time

The plotter record could be read to 0.1 min with the paper speeds generally used.

4.4.1.3 Orientation

In the apparatus involving a Dove prism,the relation between test field orientation and plotter record was frequently calibrated by having the subject turn the prism to the three positions at which the test field appeared to be horizontal, vertical and horizontal. In apparatus M_2 there was a non-linearity of about 5^o in 90^o for which rough correction has been made. The potentiometer used with M_3 showed no non-linearity.

4.4.1.4 Luminance

Two S.E.I. spot photometers were used to measure luminances. One of them had been recently calibrated against a subsidiary standard lamp. They can be read to about 0.1 log units.

4.4.2 Reliability of the subject's measurements

4.4.2.1 Hue match settings

The standard deviation about the mean of a group of hue match settings depended upon the strength of the aftereffects that the subject was matching.

For 3-4 readings on a strong aftereffect (S = 3 cm), the standard deviation was typically 11-29%, for 3-7 readings on a medium aftereffect (S = 0.7-1.3) it was 11%, and for 7 readings on a just detectable aftereffect (S = 0.23) it was 35% (see for example, error bars in figures 4, 37a). In the case of the stronger aftereffects particularly this is largely a systematic error rather than a random one. The systematic error results from the rapid decay which occurs as a result of viewing patterned light in order to make the measurements (see expecially 5.4.1, 5.3.3, 5.3.4.1). In those cases where it was possible to allow for this effect (for example figure 27) the remaining standard deviation from random sources was only 8-11% for groups of 4 readings even on a large aftereffect. This value corresponds well to the standard deviation found using the same apparatus for 4 matches to the real hue saturations of 2 and 1 layers respectively of Cinemoid 38 and 54. The standard deviation was 6% of the difference (S = 1.9 cm) between the settings.

4.4.2.2 Time

The making of a pair of hue matches takes 0.2-0.3 minutes. A group of 3 readings on one eye can be performed within 0.6 min. In the temporal studies the plotted points generally correspond to single readings or pairs of readings for the first 3 minutes and the averages of groups of 3-7 readings at later times. The uncertainty as to the time to which points on the graphs should be ascribed is thus 1-2% from about 10 min onward. From 1-10 min the accuracy is about 5%. But within the first minutes the accuracy is only 20% and so in later graphs measurement. was not commenced until after a minute had been spent in the light.

4.4.2.3 Orientation

Subjects could set the test gratings to a subjective vertical to within 2°. Studies by others (e.g. Ellis, 1976) suggest that eye cyclotorsion is less than 1°. Subjects could set the test gratings to the orientation at which they appeared most strongly tinted to ±3°.

4.4.2.4 Reliability of the overall slopes of graphs

The graphs of growth of the McCollough effect as a function of time for 13 subjects showed only a 10% variation in slope (Table 12 of chapter 5.8). For decay, however, the variability is greater (more than 20%, see for example Table 3 and figure 6 of chapter 5.1). There are two sources of this variability in the decay graphs. Firstly, as will be discussed in 5.1.2.3, 5.1.2.4 to 5 and 5.6, the uncertainty as to the zeros from which to measure the subject's aftereffect and time elapsed. Secondly, as we shall see in chapter 5.4 and 5.3.3 both the luminance and the degree of patterning of the subject's visual diet between and during readings affect the rate of decay.

4.4.2.5 Repeatability

When subjects are exposed to the identical stimuli at intervals of a week the magnitude of the aftereffect varies,apparently randomly,by about 10%.

Chapter 5. Some temporal properties of the McCollough aftereffect.

Summary: The form and the time constants of the decay and growth of the McCollough effect are investigated. Though the exact form of the decay function is the ongoing theme of the whole chapter, the following parts contribute most to the picture: experiments 5.1, 5.3.2 , 5.3.3 , 5.4.1, 5.4.4.1 section 5.5, experiments 5.5.1, 5.6.1 and 5.7.2. Sections 5.1 - 5.3 take stock of a number of factors in the inducing and decay situations respectively which might conceivably influence the rate of decay. Section 5.4 then deals in closer detail with that factor which appears to be most influential, viz. the amount of light entering the eye.

The work in this chapter is described in roughly the order in which it was performed, except that under the first experiment (5.1) some recent runs are included alongside older material to bring out distinctions which were not evident from the earlier data

Experiment 5.1. An investigation of the decay of the McCollough aftereffect in a normal visual environment.

The apparatus for presenting the stimuli and for measuring the aftereffects have been described in detail in the preceding chapter and so will be outlined here only briefly. The pre- and post- exposure measurements of the subject's orientation-contingent chromatic bias were made using the hue matching apparatus M_1 (fig. 2a, c section 4.2.1)
Test field T_2 of fig. 1 was illuminated at 0.5 log ft L on its white

stripes. The test gratings subtended 1.77 (2.49)* cycles per degree at the subject's eyes when the chin rest was at 69 (97) cm from the test field

To induce McCollough aftereffects oblique square-wave gratings at + and - 45° to the vertical were presented alternately in the same area of a screen by two projectors with a shutter (E_1) or in a four field tachistoscope (E_5) as described in 4.1.4. The light from each of the two gratings passed through a red or a green filter (cinemoid 14 and 24) placed either at the light source or at the subject's eyes. The subject used a chin rest at 95 (46) cm from the stimulus screen. The grating subtense was 2.5 (3.2) cycles/degree and the luminance of the coloured stripes of the grating 3.7 (5) ml.

Exposures were monocular or binocular. During monocular exposures the unexposed eye was covered by a black patch on elastic, or by the subject's hand. In binocular exposures using apparatus E_1 both eyes viewed the same gratings, but saw them through colour filters of the same or of complementary colours at the two eyes in different runs. For the run of 16 December 1976 (figs 3,4) gratings of the same colour and orientation were presented by the tachistoscope simultaneously to the two eyes. Exposures lasting from 1.6 to 80 min were given at various times of day to 14 Ishihara normal subjects. For most runs the exposure was continuous. In a few, exposure was interrupted 4 to 6 times for a total of 10-12 min for the taking of measurements (in the manner described in Expt.5.8.1)

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* The dimensions and particulars in brackets given in this experiment refer to a few runs, like that of 16 December 1976 (fig. 3, 4), for which the tachistoscope (E_2) was used to present the stimuli.

The subject made 1-8 pairs of hue match settings just before the McCollough exposure. At the end of the exposure he was rapidly turned to face the test apparatus again, the room being in darkness and his eyes shut. He then opened his eyes and made 1-8 pairs of hue match settings immediately (or following one minute spent in viewing a white unpatterned card at 0.5 log ftL).The subject then engaged in normal life, returning to make groups of hue match settings at intervals ranging from minutes to hours later. In most runs the periods between making these later measurements were spent both indoors and out without restriction. For a few of the later runs, from 1976 onwards the subject remained in one room lit at 1.1 or 0.5 logftL in its brighter areas. In these latter cases the steady luminance is indicated in the figure captions. Decay on 16 December 1976 was at 0.5 logftL for the first 200 min.

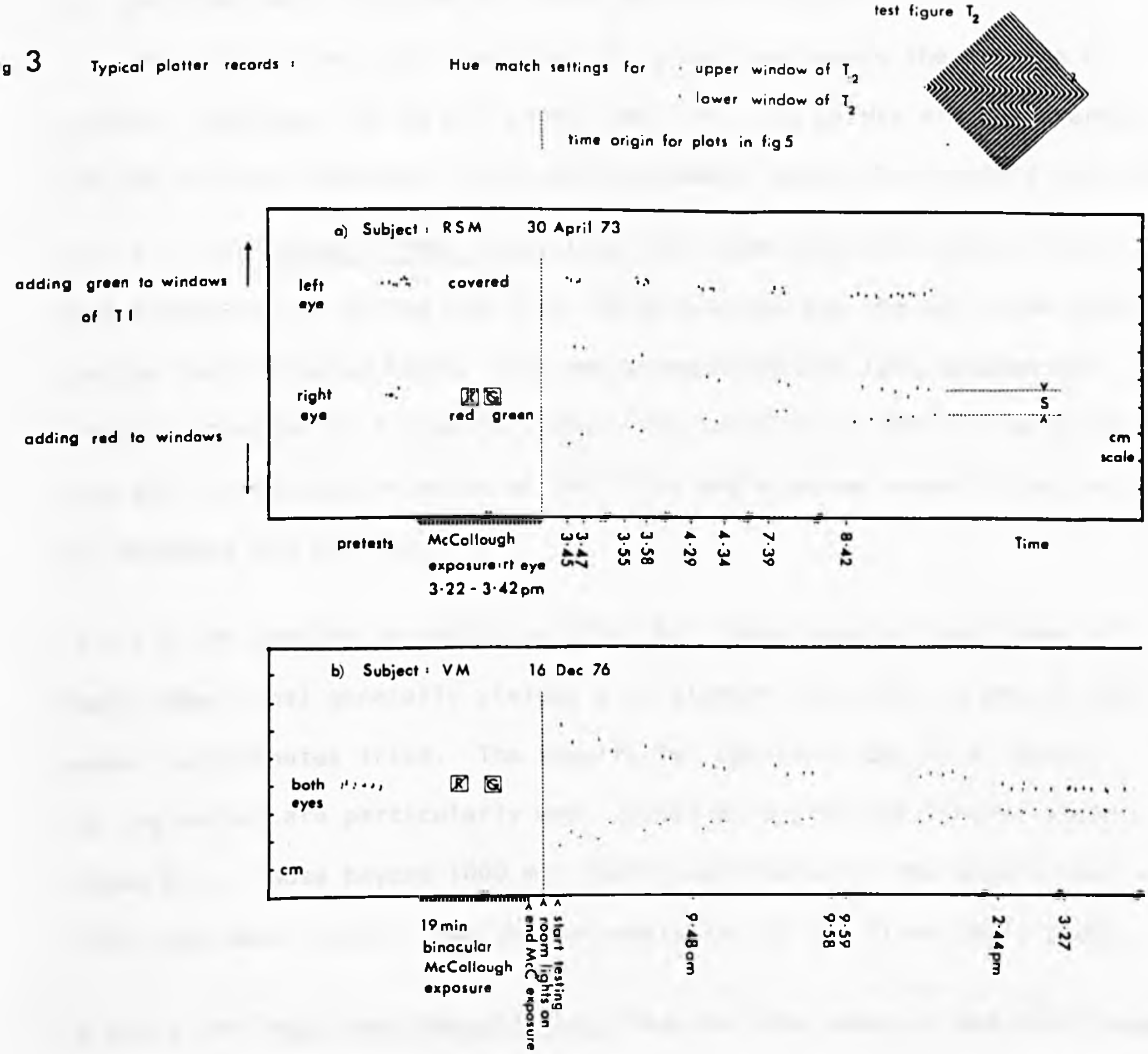
Results:

5.1.1 The form of the decay curve

Figure 3 shows typical plotter records from runs on two subjects. 3a is an entire record, 3b shows only selected samples. Time is marked on the abcissa in minutes. The positions of the pen marks on the ordinate indicate directly (see 4.2.1)the positions of the join in the red and green colour mixer which correspond to the subjects' hue matches for the achromatic test gratings at $+45^{\circ}$ and -45°. The distance S (in cm) between a pair of pen marks is taken to be a measure of the subjects' McCollough aftereffect strength at the time.

The two subjects RSM, VM had good uncorrected vision and the McCollough exposures were uninterrupted with presentation cycles of a) 6 sec on, 3 sec off, b) 9 sec on, 9 sec off.

Fig 3 Typical plotter records :



In figure 4 the results from the two runs of fig. 3 are plotted as a function of time on a variety of co-ordinates including linear/linear and log/log. Time was measured, for RSM from the end of the McCollough exposure; for VM from the opening of the eyes in the light after the end of the McCollough exposure was taken as time origin.*

For RSM the last point only of the graph represents the average of several readings, for VM all except the first two points are the average of two or more readings. Error bars represent twice the standard deviation.

5.1.1.1 The linear/linear plots (fig. 4a) show the rapid decay of the McCollough effect during the first 40-50 minutes and the very slow decay during the following hours. The gap between 500 and 1500 minutes was largely occupied by a night's sleep. The results for the following day do not fall on the continuation of the first day's curve, even if the hours of darkness are omitted.

5.1.1.2 On log/log co-ordinates (fig. 4b) these results (and those of many other runs) generally yielded a straighter line than on any of the other co-ordinates tried. The results for the first day (i.e. about 2½ log units) are particularly well fitted by a straight line of slope about 0.3. Those beyond 1000 min (which were taken on the second day) fall much more rapidly than the extrapolation of the first day's graph.

5.1.1.3 On log/linear co-ordinates (fig. 4c) the decay of the McCollough effect during the first day appears to fall into two distinct and fairly straight portions: over the ranges 0-20 min and 100-500 min results are well fitted by exponential decays with half lives of 14 and 550 min respectively (fig. 4c, also Table 4 of section 5.1.5). On closer

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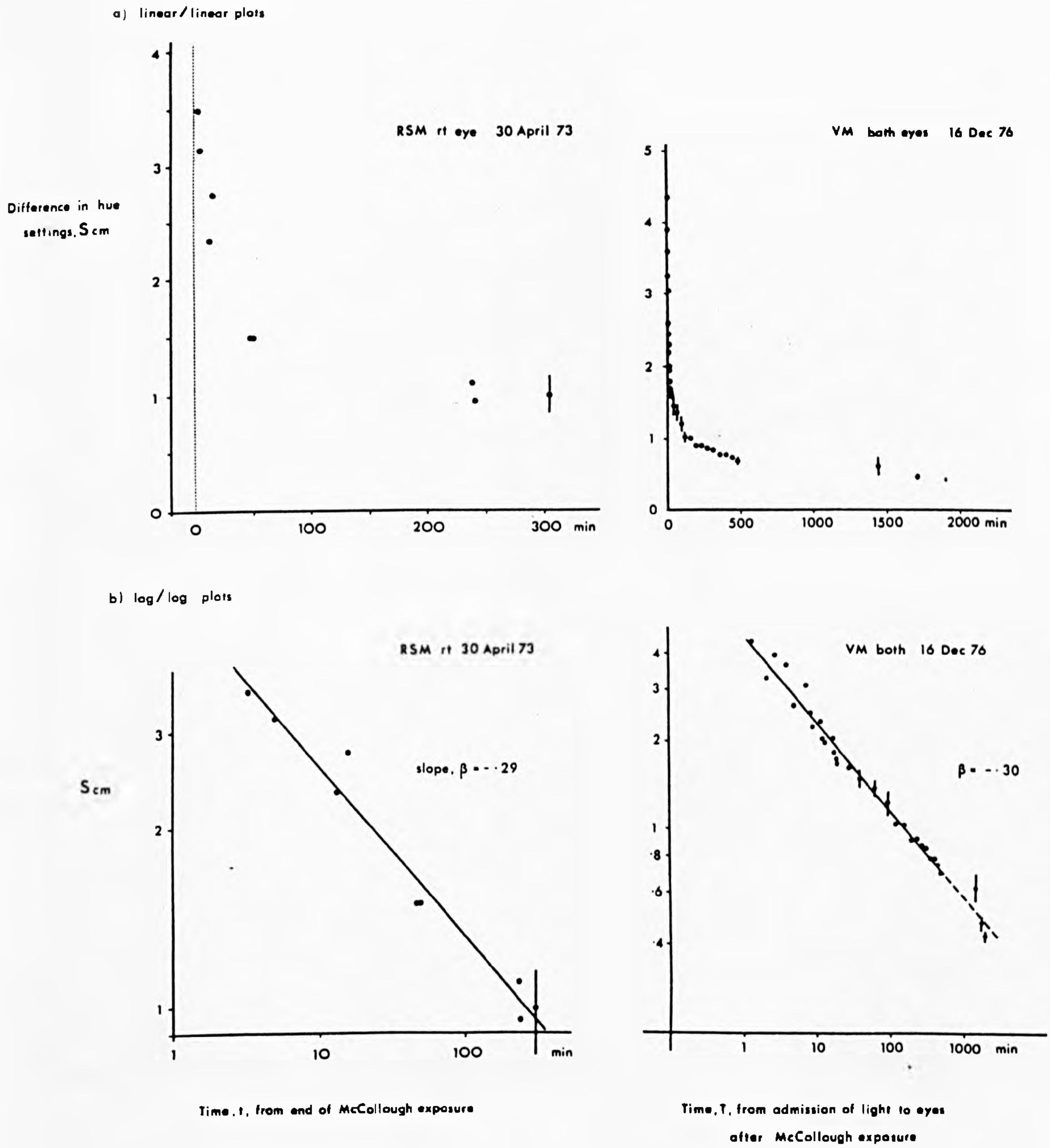
* The opening of the eyes in the light was adopted as time origin in view of the outcome of expt. 5.4.1 (see chapter 4.3.3.1). In practice the change of origin makes a difference of only 10-40 sec to any run in the present experiment because the subject was turned rapidly from exposure to measurement.

fig 4 THE DECAY COURSE of the McCOLLOUGH AFTER EFFECT

plotted on various coordinates

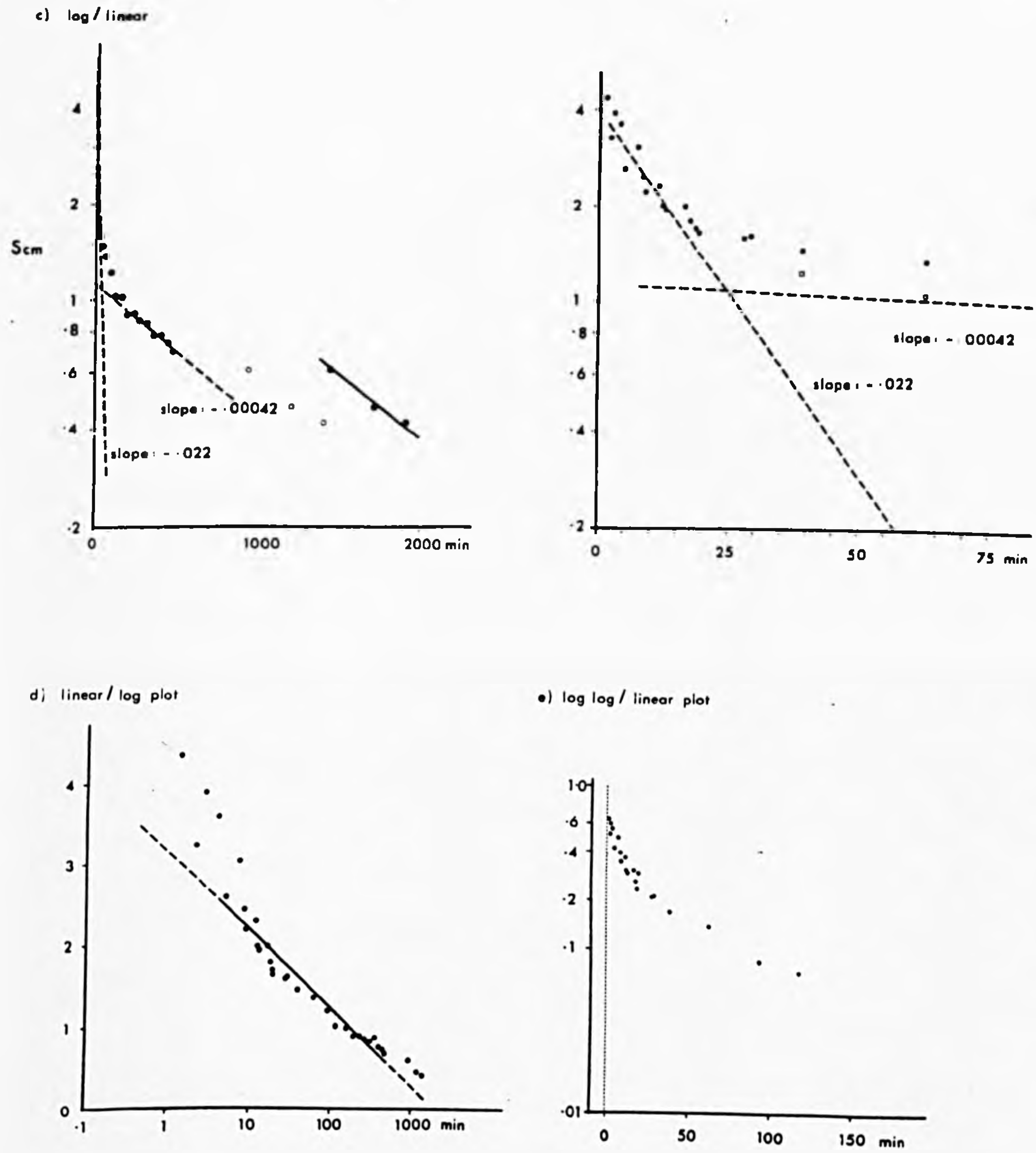


The difference, S cm, in hue settings for the two runs of fig. 3 is plotted as a function of time on the following co-ordinates:

a) linear/linear
b) log/log
c) log/linear
d) linear/log
e) log log/linear

For RSM time is measured from the end of the McCollough exposure; and for VM from the admission of light to the eyes after the end of the McCollough exposure. For RSM the time between readings was spent in the ordinary environment, for VM in a room at 0.5 log ft L until 200 min.

fig 4 (cont) VM both eyes 16 Dec 76



Error bars indicate twice the standard deviation for the means of groups of readings.

In c), o represents the positions which the second day's points would take if the dark hours of night were omitted,

□ represent the result of summing the two dotted lines of slope -0.022 and -0.00042.

inspection, however, the decay curve is not perfectly fitted by the sum of two exponentials. The replotting of the early part of the graph on an expanded time scale shows that the half life during the first 20 minutes smoothly increases from 5 to 30 min (cf. also Table 4). Moreover, the intermediate points at 25-90 min are only moderately well fitted by the sum of the two exponentials which fit the two ends of the curve. Unfilled squares show the calculated sum of the exponentials of slopes -0.022 and -0.00042. When a similar calculation was made from the early and late slopes of a further 10 runs following exposures ranging from 8-37 min, the calculated sum fell some 10-20% below the observed results in 6 runs, coincided with them for 2 and fell slightly above them for 2.

The points for the second day fall on a shallow curve of somewhat the same slope as the later portion of the first day's graph. This line does not, however, form a continuation of the first day's graph even when the period of 520 min overnight darkness is omitted (unfilled circles).

The first day's decay curve requires more than two exponentials for a good fit, and the second day's decay requires separates curve fitting.

5.1.1.4 On linear/log co-ordinates* (fig. 4d) the graph is somewhat concave. This was true for some 30 other graphs on several subjects, though some - especially those covering a smaller range of values of S - were nearly straight. Since the range covered by S is rather below a log unit in the day, the difference in straightness between the linear/log and log/log plots (above) cannot be very great. Induction times of 5 to 20 min yielded progressively steeper slopes differing by a factor of more than two whereas the values of β for the corresponding graphs differed very little (cf. figs. 6, 7).

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* These co-ordinates have been used by Riggs et al., 1974, and in most other published work (see 5.1.5)

5.1.1.5 The log log/linear graph (fig. 4e) was included as a means of testing the linearity of the apparatus. If the hue matching apparatus gave readings which were not linearly related to the subject's McCollough effect M.E., (if, for example, ME $\propto$ log S), then the taking of logs might have revealed a simpler relation between log S and time than that of fig. 4e. That the result (fig. 4e) is still a curve reassures that at least the major part of the power law curve of fig. 4a is a genuine property of the McCollough effect and not an artefact.

Conclusion

The form of the decay of the McCollough aftereffect is not simple. The second day*of decay follows a separate course from the first day, and at least three exponentially decaying functions are required to fit even the first day's results.

On the first day the half life increases smoothly from 5 min, immediately after the McCollough exposure, to 600 min, ten hours later. Decay appears to follow a power law, the majority of runs being best fitted by a straight line on log/log co-ordinates.

5.1.1.6 Discussion

Exponential processes: The possibility that, at least on the day of the McCollough exposure, there are a number of exponential processes simultaneously decaying is not, of course, ruled out by the above conclusions.

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* The effect of the first night on decay is investigated in sections 5.3, 5.4 and the second day's decay is examined in 5.5.

Mere complexity cannot be used as a criterion of what is improbable in the nervous system. It would seem indeed highly probable a priori that the exposure to pattern and to colours during presentation of the McCollough stimuli would induce several short-lived aftereffects affecting the nett perception of the test stimuli at least for a few minutes afterwards. Some later observations suggest, however, that this does not occur to any appreciable extent beyond about 10 min after the end of the McCollough exposure: In 5.4.2 it is reported that after a night's sleep the course of decay is not significantly different, from 10 to 100 min, from that immediately following a McCollough exposure. It might be countered that this arises because some of the short-lived effects of dark adaptation are fortuitously similar to those of exposure to coloured gratings but it seems more probable that the bulk of the smooth sequence of time constants is an integral part of the McCollough effect.

A power law of decay does not suggest any well known type of chemical process. This form of decay points, if anything, to a process in which the probability of certain events necessary for alteration of the aftereffect's strength diminishes as time proceeds. Their probability apparently decreases rapidly during the first hour after a McCollough exposure and gradually becomes so small that there is very little decay during the remainder of the day.

The implications of the form of the decay are further considered in 5.1.4 and in Chapter 9.

Log/log co-ordinates will be used almost exclusively from here on because on them a) the results are well fitted by a straight line, b) requiring a minimum of specifying parameters, and c) having slopes which are a dimensionless and unit free ratio which d) does not differ greatly in magnitude for a considerable range (x10) of initial magnitudes (see figs 6,7).

Some further results obtained by the methods of experiment 5.1.1 allow us to assess the influence on this slope, β, of various inter-subject differences, such as age, sex, and features of the inducing exposure, particularly its binocularity and duration.

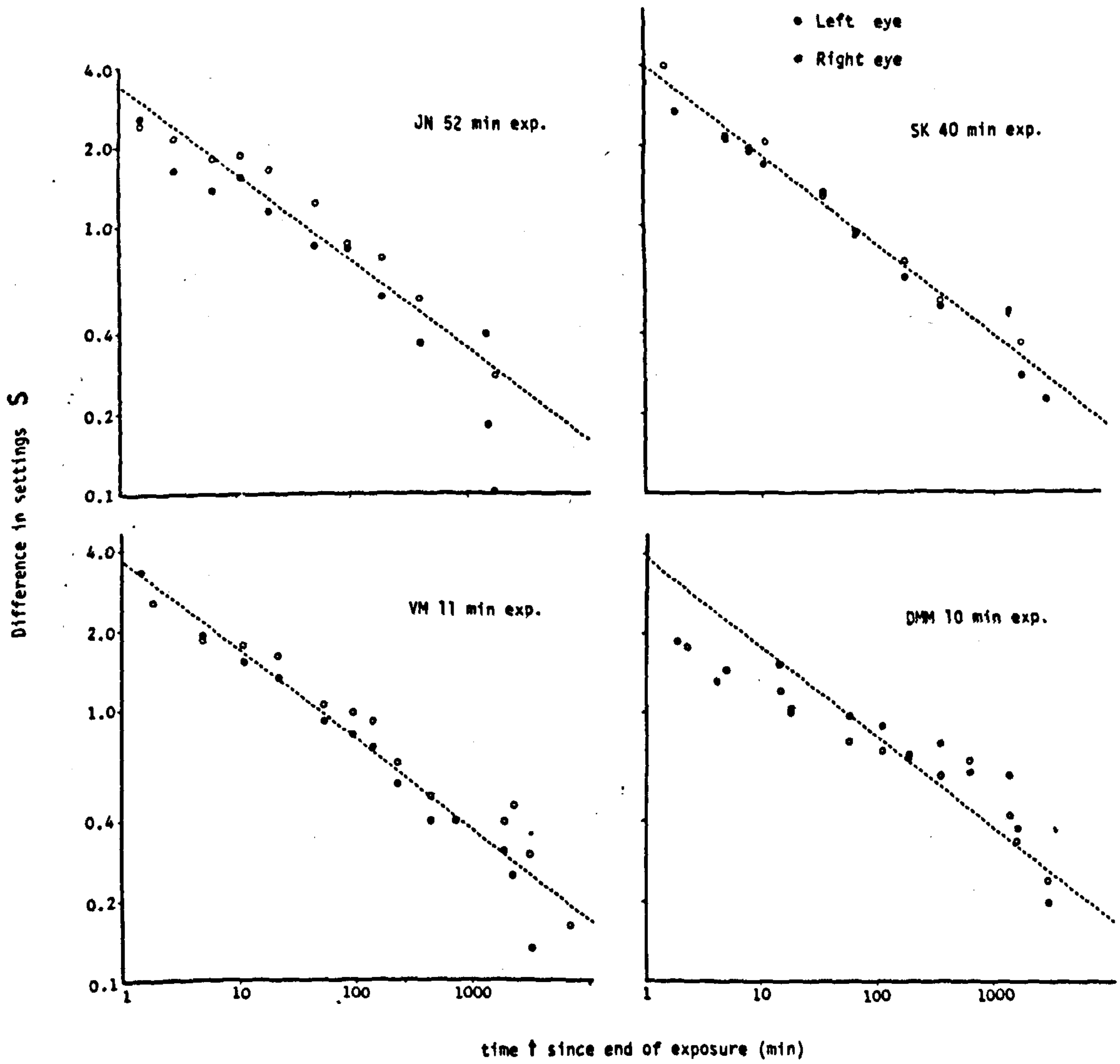
5.1.2 <u>The effect on the rate of decay of the McCollough effect of some variables of the exposure</u>.

Figure 5 shows the decay, for each eye of 4 subjects, of the after-effects induced by differing binocular exposures. JN and VM viewed the identical inducing stimuli binocularly; whereas the two eyes of SK and DMM viewed the same grating stimuli but in complementary colours. (For convenience both negative and positive values of S are plotted positively.)

For DMM the 10 min McCollough exposure was continuous, for the other 3 subjects exposure was interrupted after exposure periods of 0.6, 1.3, 2.6, 5.6 . . . min, for about 2½ min of making hue match settings. The presentation cycle was in every case 6 sec on, 3 sec off. The different durations of exposure were required to induce similar aftereffects in the four subjects.

The points in fig. 5 represent the average of 2-8 pairs of readings, fewer readings being averaged for the earlier points on each graph. A night's sleep intervened for each subject at about 1000 min.

fig 5 DECAY OF McCOLLOUGH EFFECT



Subject	Age yrs	Sex	Exposure date	Exposure end	Exposure duration	Binocular Stimulus L eye	Binocular Stimulus R eye	Slope β of the graph for first day L eye	Slope β of the graph for first day R eye
JN	22	F	4.10.73	10.58 am	52 min	G R	G R	.30	.26
SK	40	M	20.9.73	11.10 am	40 min	R G	G R	.32	.37
VM	39	F	29.10.73	8.29 am	11 min	G R	G R	.37	.27
DMM	51	M	18.9.73	11.40 am	10 min	G R	R G	.26	.19

The dotted comparison lines have a slope of -1/3. The values of the average slope,

$$\beta = \frac{\log S_1 - \log S_2}{\log T_1 - \log T_2}$$

for the first day of the decay are given in the table below the graphs in fig. 5.

Table 3 gives the values of β for similar runs on 12 subjects* in which

a) one eye was exposed the other being covered,

b) both eyes viewed the identical stimuli simultaneously, and

c) the two eyes viewed grating stimuli which differed in colour.

The runs for which the inducing exposure was interrupted are marked with a cross (+). The values of β for the first day are based on a minimum of 8 groups of readings, those for the second day on only 2 or 3 groups of readings. Time origin is the end of the McCollough exposure (or exposure to light a few seconds thereafter, see footnote to 5.1.1.

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* There were seven further subjects whose results are not included; three because their uncorrected vision proved to be very poor, three aged 64, 30 and 7 years because their colour matches had a large scatter for other reasons and one because her aftereffect was very small. Their results all nevertheless showed the same general trends observed in the other subjects.

Figure 5: The decay of McCollough aftereffects induced by the various binocular stimuli specified in table below graphs. The dotted comparison lines have a slope of -1/3. A night's sleep intervened at about 1000 min for each subject. The values of the slope, $\beta = \frac{\log S_1 - \log S_2}{\log T_1 - \log T_2}$, for the first day's decay are given in the table.

Table 3. The rate of decay of the McCollough effect as a function of binocularity of the inducing exposure and other variables.

Subject			age (yrs)	Exposure: duration (minutes)	presentation cycle: on	off	end	Aftereffect: log/log slope β	1st day	2nd day (approx.)
a) Monocular exposures										
JEM	7.7.73	F	13yr	20min	15sec	7sec	9.10 am	L	-.33	
RSM	30.4.73	M	16	20	15	7	3.42 pm	R	-.30	
MAS	10.5.73	F	28	22	8	4	4.27 pm	R	-.35	
VM	5.2.73	F	38	20	15	7	9.50 am	R	-.34	-1.1
VM	13.8.73	F	38	20	15	7	9.00 am	L	-.26	-2.3
b) Binocular exposures: identical stimuli to the two eyes										
KB	8.10.73	M	26	20	6	3	12.58 pm	R	-.29	-.15
								L	-.44	-5.2
KB	2.11.73	M	26	11	6	3	9.30 am	R	-.29	-3.1
								L	-.21	
KB	1.10.73+	M	26	11	6	3	11.35 am	R	-.53	
								L	-.30	
VM	6.11.73	F	39	12	3	2	12.46 pm	R	-.31	-3.6
VM	29.10.73	F	39	11	6	3	8.29 am	R	-.27	
								L	-.37	
VM	14.2.77	F	42	20	9	9	9.47 pm	R	-.30	
								L	-.38	
JF	28.10.73+	M	26	11	6	3	10.08 am	R	-.28	
								L	-.26	
MR	30.10.73+	F	25	25	6	3	10.21 am	R	-.40	
								L	-.43	
JN	4.10.73+	F	22	52	4	2	10.58 am	R	-.26	-1.6
								L	-.30	-3.0
c) Binocular exposures: different stimuli to the two eyes										
VM	9.12.76	F	42	20	9	9	12.16 pm	R	-.20	-1.2
								L	-.29	-2.6
DM	19.9.73	M	27	15	6	3	11.17 am	R	-.27	
								L	-.26	
JPW	19.9.73	M	35	15	6	3		R	-.35	
								L	-.24	
DMM	18.9.73	M	51	10	6	3	11.40 am	R	-.19	-1.9
								L	-.26	-6.1
SK	20.9.73+	M	40	40	6	3	10.40 am	R	-.37	
								L	-.32	-2.0

+Interrupted exposures

Figure 6 shows β as a function of binocularity and duration of the exposure for one subject and figure 7 shows runs typical of those summarised in figure 6.

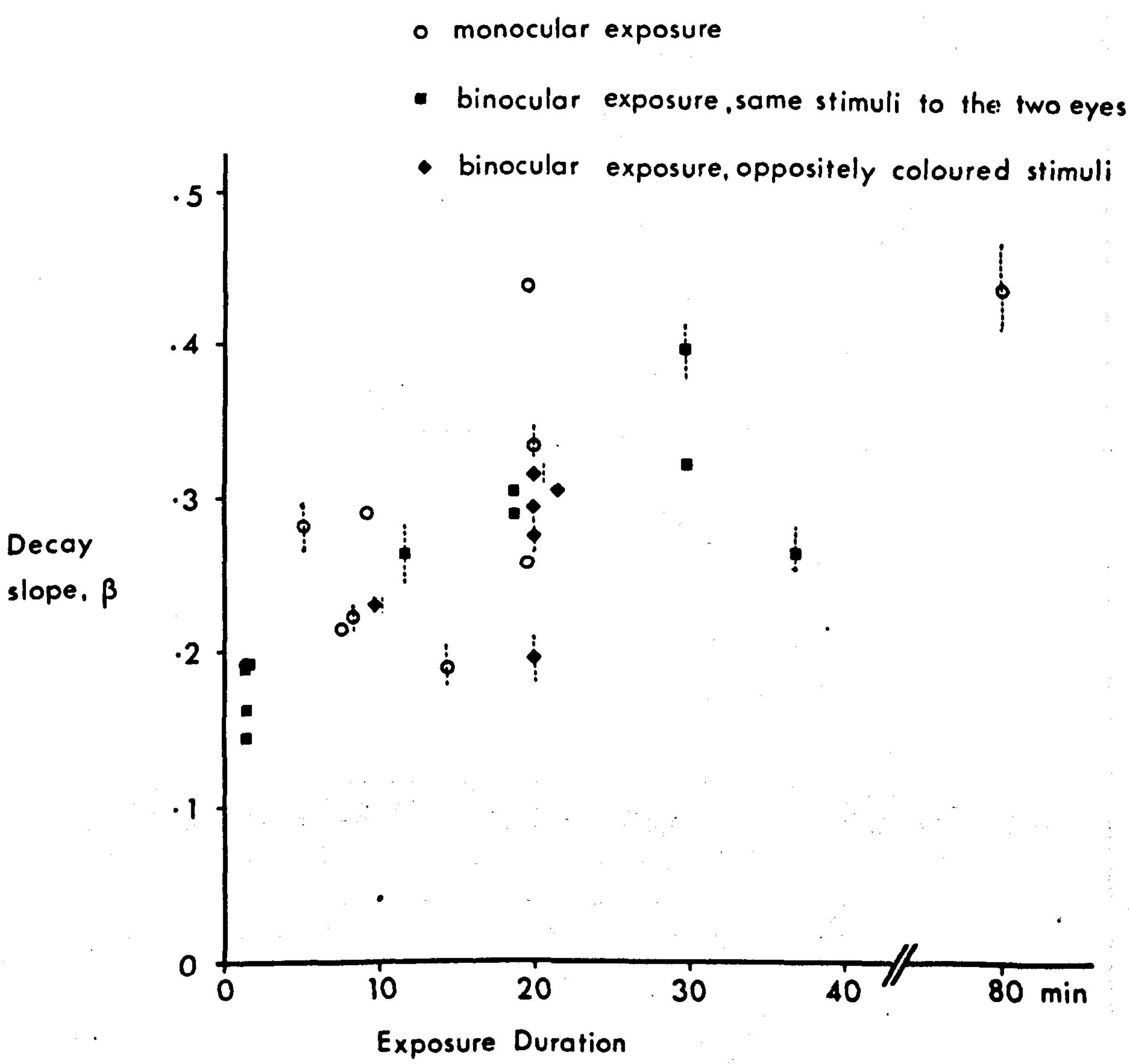
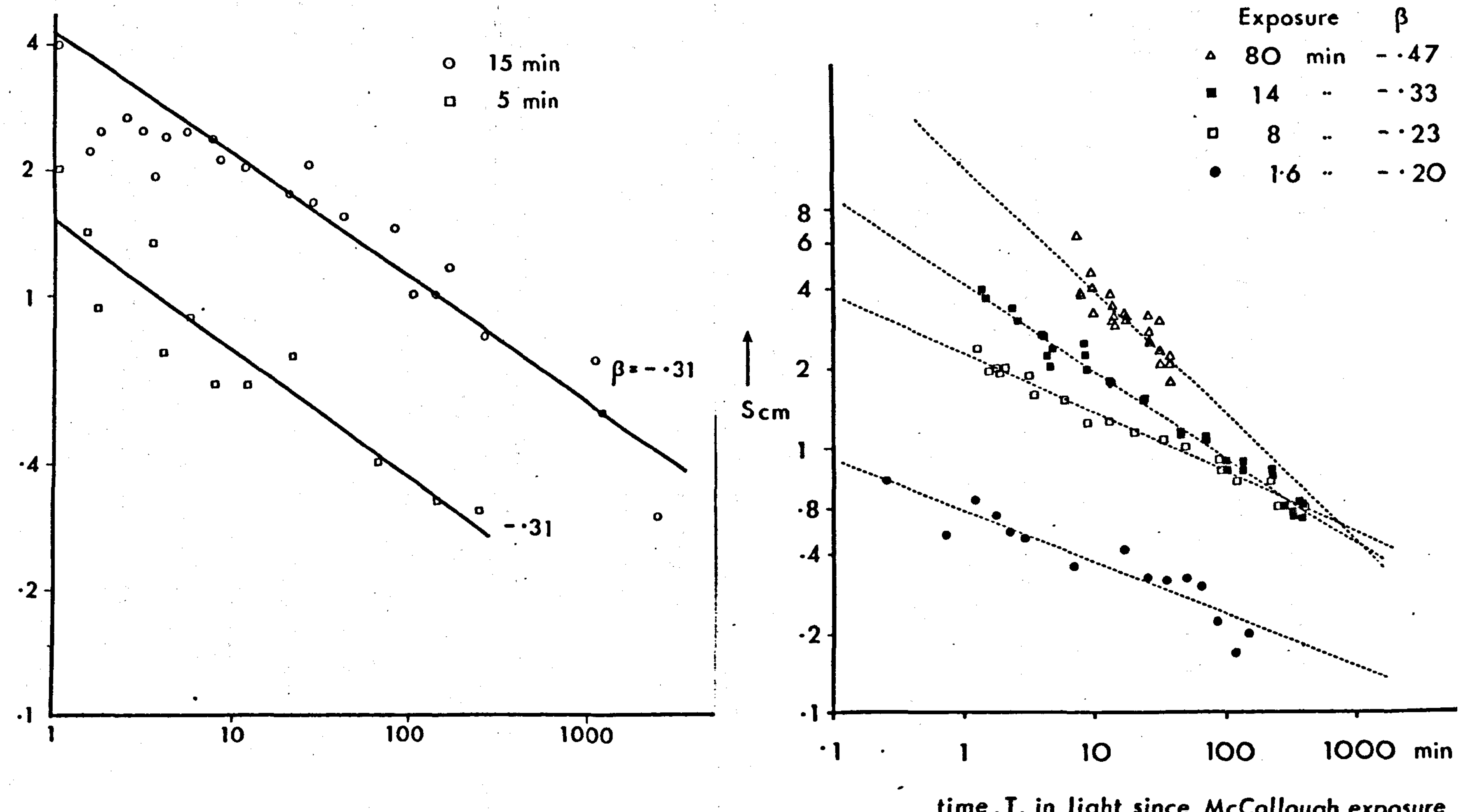


Figure 6: The rate of decay of the McCollough effect as a function of the duration and the binocularity of the inducing exposure.

Figure 7: Decay of the McCollough aftereffects produced in one subject by exposures of various durations.



Findings:-

5.1.2.1 Binocularity:

The slope of the decay course of the aftereffect in one eye is not obviously or interestingly affected by the simultaneous decay of a similar or opposite effect in the other eye. (This conclusion is confirmed by Expt. 6.3.1)

In general the decay of the aftereffect seen by each eye was found to proceed quite independently of events taking place in the other.

It is not possible to be so definite about the other variables since there is less systematic evidence, but some general points must first be made about other factors which affect the slope.

5.1.2.2 Causes of variation in β: general discussion

The slope β of the decay of the McCollough effect for the above 12 subjects ranges from -0.19 to -0.47 with an average of about -0.30 $\pm$ 0.07 for the first day. For the second day the slope is some ten times greater on the same co-ordinates.

The most striking feature of table 3 is that the difference in slope between graphs for the two eyes of one subject (following binocular exposure) can differ by as much as half the total range of values covered by all the subjects under all conditions. The origin of these inter-ocular differences is not entirely clear. But the following general sources of uncertainty which affect all runs have been identified.

The slope of a log/log plot is of course highly sensitive to uncertainty as to the zero to be taken on either or both axes.

5.1.2.3 Subject's initial bias

β is sensitive to the subject's initial bias. No correction has been made for this bias in the above results because the manner in which the bias behaves when a McCollough exposure is administered can only be guessed at (see 5.7).

The effect of a bias upon slope if the bias is in fact decaying much more slowly than the new effect can be judged from the following two examples. Subject MAS (table 3) had a large pre-exposure bias (of -0.45 cm) resulting from an opposite McCollough exposure on the preceding day. If this is assumed to remain constant throughout the hour or so for which decay was measured, the value of β becomes -0.24 instead of -0.35. Similarly the initial bias for VM for the 14 min run of fig. 7b was +0.13. When this is deducted from all readings the slope becomes -0.30 instead of -0.33. Because such large uncertainties are introduced by initial bias, runs were generally not performed if the subject was found to have a bias of above 0.15.

5.1.2.4 Time origin

β is similarly sensitive to the placing on the time axis of the readings for the first two or three minutes. Small uncertainties as to the exact moment at which a subject began to look at the test card are therefore not unimportant. If, as seems likely from fig. 10 the moment by moment light level entering the eye affects the decay rate, then alternate covering of each eye in a darkened room while readings were made with the other will have the effect of making the graph spuriously shallow for the first few minutes and steep later. Graphs where a large number of readings were gathered in this way during the first few minutes have been excluded.

It was not at first obvious why the time origin should be taken at the end of the exposure rather than at some suitable average point during the exposure. But it was found that values of β became much more diverse as soon as the time origin was moved back in time. A further indication that a time origin near the end of the McCollough exposure was appropriate was the fact that the interrupted and uninterrupted exposures led to much the same decay slopes. In view of expts. 5.4.1, 5.6.1 the moment at which the subject opened his eyes after the end of the exposure has, as nearly as possible, been taken as time origin.

5.1.2.5 Random variations

Apparently random fluctuations of the readings about their mean course are considerable. They are much reduced by keeping the subject at a constant luminance level. Because of this variability the omission of even one point near either end of a graph can strongly affect the value of β. Error bars in fig. 6 indicate the magnitudes of such variations in slope. (≑ 5%)

5.1.2.6 Possible systematic causes of alteration in β: subjects and exposure conditions

Given the breadth of uncertainty introduced by the above factors, β cannot be said to be significantly affected by any of the variables shown either in figure 5 or in table 3 i.e. the age or sex of the subject, the degree of binocular unanimity of the inducing stimuli, the time of day at which decay occurred (see further comparisons in section 5.3.6.2) the length of the on/off presentation cycle, or interruption of the exposure. There is also in fig. 5 and table 3 no evident influence of the duration of the McCollough exposure, but it must be pointed out that the range of inducing times is not great (x4) and that those subjects who were given the longer exposures (notably SK and JN) required them in order to reach the same initial aftereffect strength as the other subjects. The fact that their decay rates are so similar to those of VM should then perhaps be taken simply as an indication that effects of similar initial strength decay at similar rates rather than as showing that decay rate is independent of exposure duration. The indications from Figs. 6 and 7b are that β is not constant but increases by a factor of 2 for the tenfold increase in initial strength resulting from a 50 fold increase in exposure duration.

5.1.3 Summary

In 1972 (MacKay and MacKay, 1973) we communicated to the Physiological Society the log/log plots of figures 5 and 7a and the conclusion that our results were well fitted over most of the decay course by a straight line, of about -1/3. We stated, on the basis of exposures lasting 5-15 min, that "a shorter exposure yields a lower line of the same slope" (fig. 7a). And "Over most of its course the strength of the McCollough effect (S) is a negative power function of the time (t) from cessation of adaptation,

$$\frac{S}{S_o} = \left(\frac{t}{t_o}\right)^{-\beta} * \qquad \text{where } \beta \simeq 1/3"$$

For 12 subjects, after inducing exposures of 10-50 min, the average value of the slope β during the day on which the exposure occurred was

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* Elsewhere I have defined by $\frac{S_1}{S_2} = \left(\frac{t_1}{t_2}\right)^{+\beta}$.

β therefore takes negative values in all tables etc.

0.30 ± 0.07. There is no obvious variation of β with the age or sex of the subject, with the degree of binocular unanimity of the inducing stimuli or the time of day.

These conclusions are still valid when the following three refinements are added:

5.1.3.1 The term 'most of its decay course' must be restricted to the first day's decay. Only later did we perceive that following an overnight hiatus the results not only fall faster, but fall on a separate nearly straight line (e.g. section 5.5).

5.1.3.2 In view of the results in 5.3 and 5.6 we would now consider it more correct to say that the time origin is the time at which light began to enter the eye after the end of the McCollough exposure rather than the time at which the exposure ceases. (In our early experiments this distinction made no noticeable difference to the plots, being less than 0.3 min.)

5.1.3.3 When a large range of exposure durations (50 fold as against our original 3 fold) are explored the slope β is not strictly the same but increases with initial aftereffect strength, covering the range -0.19 to -0.47 for exposure periods of 1 to 80 min.

5.1.4 <u>Implications</u>

The theoretical implications of these findings have been touched on in 5.1.1.6 and will be dealt with in conjunction with later results in ch 9.3.1 . It is sufficient here to say that the duration and the non-exponential form of the decay course reported above seemed to point away from McCollough's original (1965b) idea that her aftereffect was evidence of the selective adaptation of single units sensitive to colour and orientation. For no unit recovery curves with such long time courses had been observed physiologically. As an 'attractive alternative' my husband, in 1973, postulated 'cooperative changes at synaptic or sub-synaptic levels, throughout an "associative network" of units'. Since, in such a network, orientational sensitivity would develop in response to the incoming patterns of events, orientation-selective units are not a necessary part of this explanation and 'the site of the adaptation could even be retinal'. (MacKay and MacKay, 1974a.)

5.1.5 <u>The form of the time course of decay of the McCollough effect: Comparison with other authors</u>.

In 1973 Riggs, White and Eimas described the decay function following exposures of 15 sec - 17 min as "nearly linear on log-log coordinates". They later (1974) published linear/log plots showing the decay over 5 days of the aftereffects of exposures lasting 5-120 min and their revised conclusion was that the majority of their curves were "nearly linear on their semilogarithmic plot". Their results for later days (one reading per day) are indeed well accommodated by these coordinates, falling on the same, somewhat concave, course taken by the first day's results. When, however, their results for the first day are plotted on log/log coordinates they yield graphs which are as straight or straighter than those on the semi-logarithmic coordinates. For five of these, corresponding to induction times of 5 and 25 min, the slope β is 0.39 ± 0.06 (see table 4). The range of values covered in the first day is 0.7 of a log unit, as we too found.

Riggs et al. (1974) show (in fig. 4) very convincingly that the decay slope on linear/log coordinates, $\left(\frac{-dP_c}{d(\ln t)}\right)$, is a linear function of the strength P_c at t = 1 min. This is a result to be directly expected from our expression, $\frac{S}{S_o} = \left(\frac{t}{t_o}\right)^{-\beta}$, if β is constant over a range of initial values of S (i.e. of P_c). For differentiation of this gives $\frac{dS}{d(\log_e t)} = \frac{-S}{\beta}$

Their straight line graph suggests that β is constant for all initial magnitudes of below 5% saturation. (Their apparatus was unable to cancel stronger aftereffects.)

The slope, $\frac{-dP_c}{d(\ln t)} \times \frac{1}{P_c}$, of the straight line in their fig. 4 should on the above calculation be = $\frac{1}{\beta}$. Its value in fig. 4 is in fact +1.2, but if Riggs et al. calculated $\log_{10} t$ though they wrote 'lnt', this slope is too large by a factor of $\log_{10} e$ (i.e. 0.434) and β becomes +0.36. This value agrees with the values of β I have calculated from their graphs of fig. 2 (and concurs with our own typical values for β).

Though their (1974) conclusions differ from ours, the results of Riggs et al. confirm their own 1973 abstract and support our conclusion that the decay of the McCollough effect is a power function with exponent about -1/3.

Shute (1977b) gives a power law expression for the decrement of the aftereffect. "The decrement d below initial strength ME_o after t minutes . . . forms the cubic hemi-parabola, $d = at^{1/3}$". "For this subject . . . $a = \frac{ME_o}{12}$" (t being presumably measured in minutes).

For large values of t this expression clearly does not represent the actual aftereffect well; the observed aftereffects as reported by every paper cited in this section do not in fact cross the zero to take negative values beyond about 28 hours. But since the mathematical approximation $\frac{t}{c}^{1/3} \simeq 1 - \frac{t}{c}^{-1/3}$ holds over a considerable range of values of t to either side of $(\frac{c}{2})^3$ it is obvious that within this region Shute's expression and ours will both fit the same results acceptably. When c is in the region of 12, Shute's expression for the fractional decrement, $\frac{d}{ME_o}$, and ours $(\frac{S_o^* - S}{S_o})$ fall within 10% of each other from 55-550 min, and within 20% of each other from 35-660 min. When Shute therefore describes our expression as having "quite a different shape" from his, this difference is significant (as far as the first day is concerned) only during the first half hour or so of the graph, i.e. when hues are most saturated. This suggests that differences in the hue matching techniques may be responsible for the divergence of his and our results. In this region Shute's expression gives lower values of the saturations than ours. This could possibly be because with no comparison area and only one colour (see 2.9.4.4 for account of apparatus) his subject's hue zero drifts.

Since Shute (1977) has given the impression that our results are anomalous as compared, not only with his own (unpublished) ones, but also with those of Riggs et al. (1974), table 4 has been prepared to facilitate comparison of the published runs. The half life at various times after the end of the McCollough exposure has been calculated, as well as the log/log slope, to characterise the decay function. Given the scatter of the

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* S_o, in our expression is the magnitude at any time t_o: t_o is not necessarily small.

Table 4 Comparison of results of Riggs et al., 1974 and MacKay and MacKay, 1975, 1977a.

Subject	Exposure Duration	β 1st day	Half life in min. at various times after induction					
			1-20	1-5	5-10	10-20	30-80	100-500
KW	5 min	-0.39				51	100	430
KW	25 min	-0.49					90	530
LR	5 min	-0.32	29				100	400
LR	25 min	-0.38				46	160	350
PE	25 min	-0.35	24	9.6	29	29	73	460
VM fig. 8 (fig. 3c of M & M 1975)	5 min 6 Sept. 1973	-0.29	18	5.5	7		170	1800
	15 min 11 Sept. 1973	-0.17	27	9	22	31	110	300
RSM Right eye Fig. 2 of M & M 1977a	20 min	-0.43	21			15	180	300

individual readings used to calculate the half lives there seems to be very little difference between the results from the two groups.

Skowbo, Gentry, Timney and Morant (1974) have two graphs showing what, at first sight, appear to be very much shallower decays in the natural environment than that of MacKay and MacKay (1975) and Riggs et al. (1974). Allowance must, however, be made for the fact that their first readings were made after 7 or 12 minutes' exposure to "homogeneous fields" (in their Experiments I and II respectively). In table 5 the decay which they observed between their first and last readings is therefore compared with that occurring over the corresponding portions of the graphs of Riggs et al.

Table 5. A comparison of the decay observed between
a) the 7th and 92nd minutes
b) the 12th and 74th minutes
after the end of McCollough exposure by Skowbo et al. ('PAS natural'), Experiments I and II respectively, Riggs et al., 1974 (subjects KW, LR and PE), and ourselves.

a)

Subject McCollough exposure time	Skowbo 1 10 min	KW 5 min	LR 5	LR 25	PE 5	PE 25	VM 12 min
a-e after 7 min	100%	>2.4	2.2	>5	1.0	2.7	1.4
a-e after 92 min	70%	1.2	1.1	2.5	0.6	1.1	0.6
decrease as % of a-e at 7 min	30%	50	50	50	40	60	60

$\beta = -0{\cdot}14$

b)

Subject McCollough exposure time	Skowbo 2 10 min	KW 5 min	KW 25	LR 5	LR 25	PE 5	PE 25	VM 10
a-e after 12 min	100%	2.2	>6	1.8	4.2	0.8	1.9	1.2
a-e after 74 min	>90%	1.4	4.0	1.3	3.3	0.8	1.2	0.6
decrease as % of a-e at 12 min	<10%	30	30	25	25	0	30	50

$\beta = -0{\cdot}06$

and two runs similar to those of MacKay and MacKay (1975).

The percentage drop in aftereffect observed by Skowbo et al. is thus comparable with that found in Riggs' subject P.E., for whom the aftereffects are systematically small.* It is possible that Skowbo et al.'s three

* The link between a small aftereffect and a small percentage rate of fall is evident from the results of Riggs et al. and MacKay and MacKay; it follows from the expression $\frac{S}{S_o} = \left(\frac{t}{t_o}\right)^{-\beta}$, that $\frac{dS}{dt} \propto S_o$.

subjects all had weak McCollough effects. But it is more likely that some aspect of their method of making hue matches using the eye which is <u>not viewing</u> the McCollough test figure gives a somewhat different measure of the effect from that of Riggs et al. and MacKay and MacKay.

Jones and Holding (1975) show a decay curve extending over 5 days which represents the averaged results from 16 subjects following 15 min McCollough exposures. It is slightly concave on linear/log coordinates, resembling the graphs of Riggs et al. (1974). But for the first 8 hours of its course the slope, β, on log/log coordinates is about -0.08. This very low value (and other features of Jones and Holding's results which will be discussed in 5.6.1.6) can be accounted for if Jones and Holding's readings for the initial aftereffect strength are spuriously low. Two features of their measuring technique may have led to low readings, expecially for the more saturated aftereffects; during testing each subject was a) presented, apparently, with only one of the two possible orientations of test grating (p. 324 col. 2), and, b) provided with no steady comparison area while he rotated 'the color mixer until the white lines in the slide appeared as colorless as he could make them'. It is likely that the subject's sense of what is 'colourless' will have drifted towards the colour he is viewing.

<u>Summary</u>

The results of Riggs et al. (1974) are closely similar both in form and in magnitude to those described in MacKay and MacKay, 1975 and in experiments 5.1, 5.1.2. The results of Skowbo et al. (1974) and of Jones and Holding (1975) were obtained by other methods of hue matching or cancellation and show shallower slopes.

Experiment 5.2 To investigate whether the rate of decay of the McCollough effect is different according as the effect is induced by a red or by a green grating.

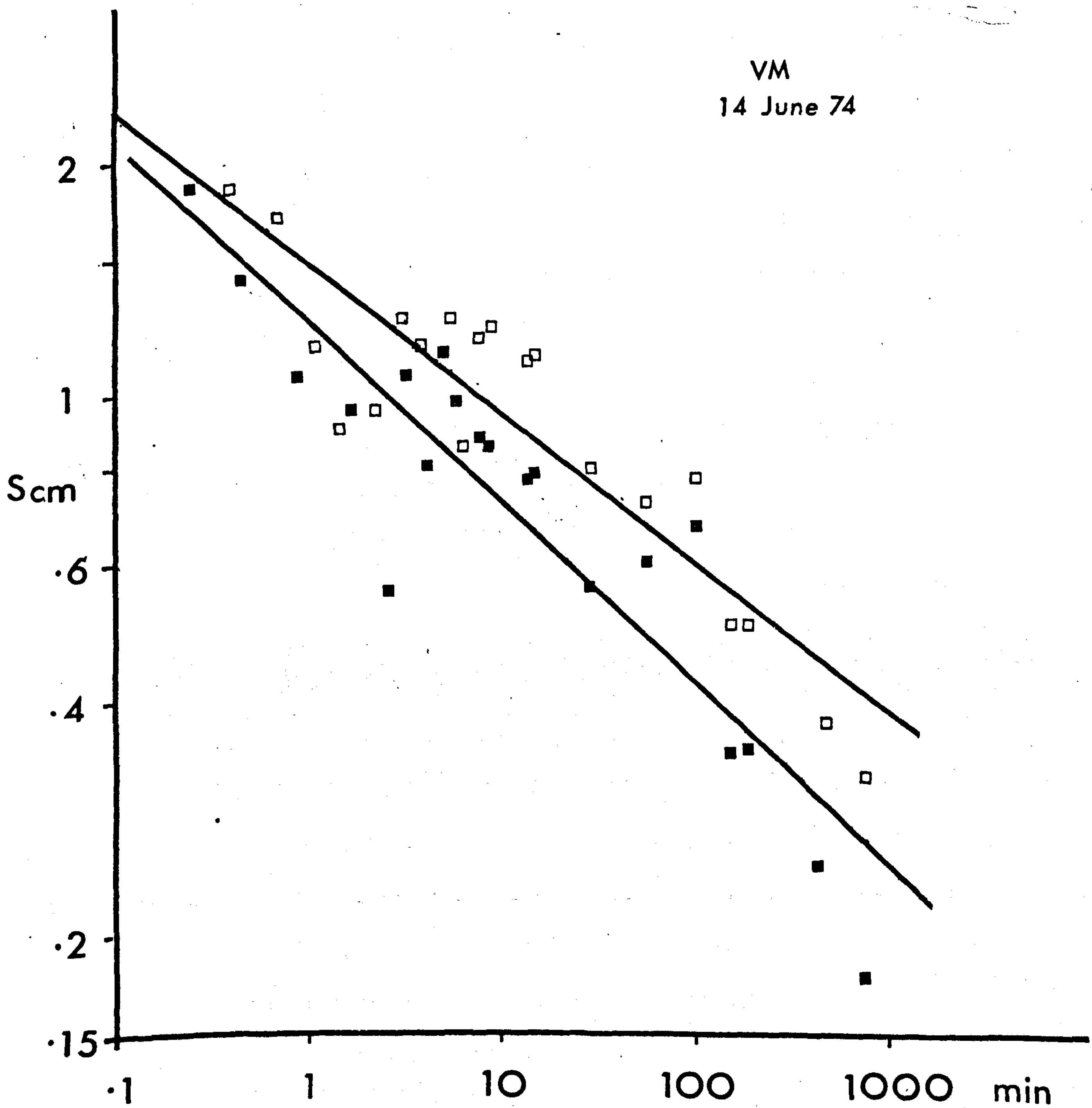
Apparatus: For the measurement of the aftereffects the apparatus and methods were exactly as in the preceding experiment. Apparatus MI with test field TI at 65 cm was used to make hue match settings using the left and right eyes alternately.

Inducing stimuli: A single left-oblique square-wave grating of 2·5 cycles/degree was presented continuously for 12 min on a screen at 95cm in front of the subject. The subject viewed this with left and right eyes alternately (for 6 sec apiece) through one layer of red and 3 layers of green cinemoid filter respectively. A black shutter automatically covered each eye alternately in a darkened room.

Results: Figure 8 shows, on log/log coordinates, the readings for the aftereffects obtained for each eye as a function of time since the end of the McCollough exposure. (All the readings occurred on the same day, the McCollough exposure being from 9.10-22 a.m.)

Findings: The magnitudes of the aftereffects in the two eyes and their rates of decay are similar. Differences as large as that between the two eyes' results occur in control runs when the two eyes receive identical McCollough exposures (cf. figure 5).

Figure 8 Decay of the orientation-contingent aftereffects produced by viewing a grating in ■, red, □, green light with the right and left eyes respectively. The slopes, β, of the log/log plots of S against time since end of McCollough exposure are -0.24, -0.19 respectively.



The magnitude of these effects induced by a red grating alone and a green grating alone is roughly half that induced by the full McCollough stimulus (of two orthogonal gratings in complementary colours) in a similar time. (See, for example, figure 9 in which the ordinate is at t = 1 min, and for which the presentation cycle was 3½ sec on 2 sec off.) Chapter 8.1.2 (figure 35) returns to the idea of 'summation' of orthogonal aftereffects.

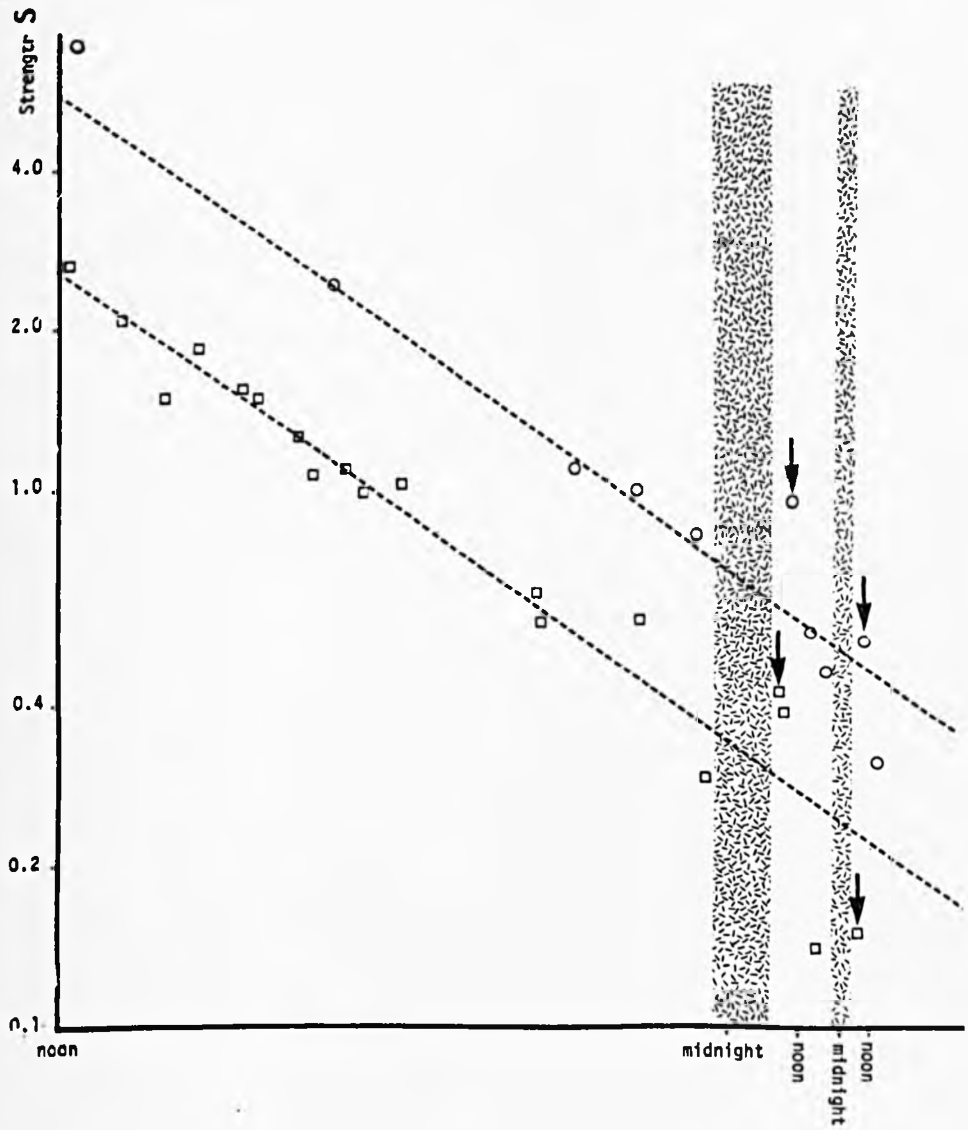
Conclusion: The systems modified by exposure to red and exposure to green gratings so as to produce a McCollough effect do not differ in any striking respect. The initial magnitudes of the aftereffects and their subsequent course of delay were highly similar.

5.3 Factors influencing the rate of decay of the McCollough effect: variables of the post exposure situation.

The variables which will be explored are the amount of light entering the eye, the degree of patterning of this light and its colour.

As mentioned in section 3.2.2 we had often noticed that the McCollough aftereffect hues looked fresher and stronger at the start of a new day at the laboratory than they had done the previous evening. The undiminished or even increased readings tallied with this impression (see Figure 9). To find out how far this increased reading was attributable to improved signalling of the test field and how far it reflected the state of the McCollough mechanism, a large aftereffect was induced in the evening so that the overnight portion of the graph should occur when the effect was some four times stronger than in figure 9.

Figure 9 Typical examples of time-course of McCollough effect over 2 days and nights (for same subject as in Figure 3) on different occasions with initial exposures of 12 min (□) and 20 min (○). Note apparent arrest of decay overnight (arrows). Scales of time and strength are logarithmic. (From MacKay and MacKay, 1975.)



Experiment 5.3.1 To investigate the decay of the McCollough aftereffect during sleep and darkness.*

Apparatus: The pre- and post- exposure measurements were made using apparatus M_1 with test card T_1 at 65 cm.

The McCollough stimuli consisting of red and green oblique gratings (2.2 cycles/degree) were presented by two projectors with a shutter (E_1) with a timing cycle of 6 sec on, 3 sec off. The subject's right eye was exposed for 25 min and then both eyes viewed the same stimuli for a further 12 min. A bed had been placed in the room beside the apparatus.

Immediately 12 pairs of post exposure measurements had been made on each eye, the subject went to bed and slept. The room was thoroughly blacked out and the room lights were turned off from the commencement of the pretest until 9.37 the following morning.

The subject awoke three times: at just before 4.13 a.m., 7.40 a.m. and 9.34 a.m. Each time, the apparatus was switched on, and when it had warmed up the subject made hue matches for about 7 minutes, noted the time, and - on the two earlier occasions - returned to bed and sleep.

Results: Figure 10 (a) shows a linear/linear plot of the aftereffect (Scm) in the left eye as a function of the time in hours since the end of the McCollough exposure. A typical decay course in the light is included, dotted, for comparison. Figure 10(b) on log/log coordinates gives the above results for the left eye and also those for VM's right eye and for both eyes of another subject, DMM. (The latter results were obtained using a portable variant of the hue measuring device in a similar overnight run). Figure 10(c) shows the results for the three graphs of figure 10(b)

* Experiments 5.3.1, 5.3.2 were published in MacKay and MacKay, 1975b.

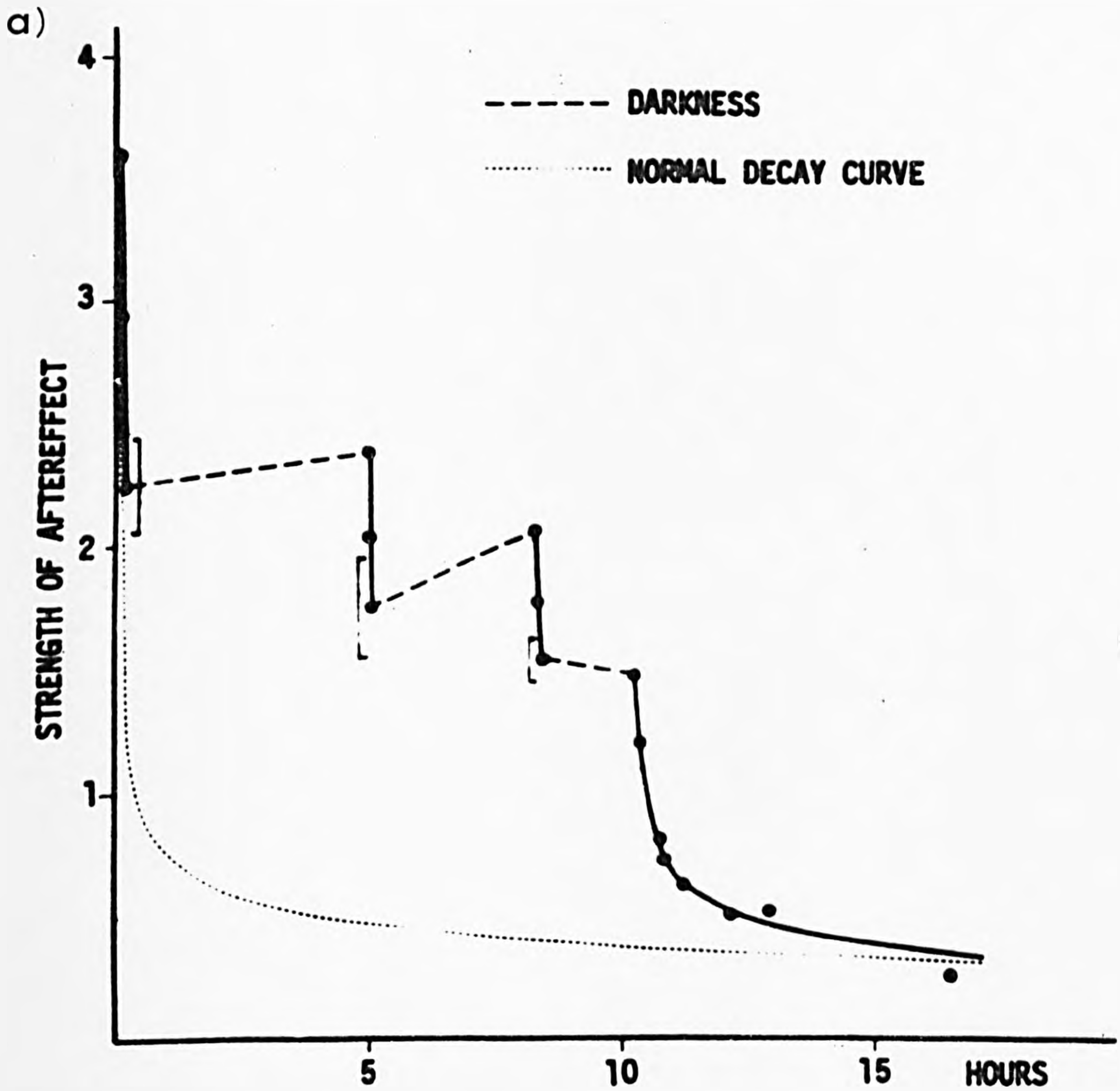
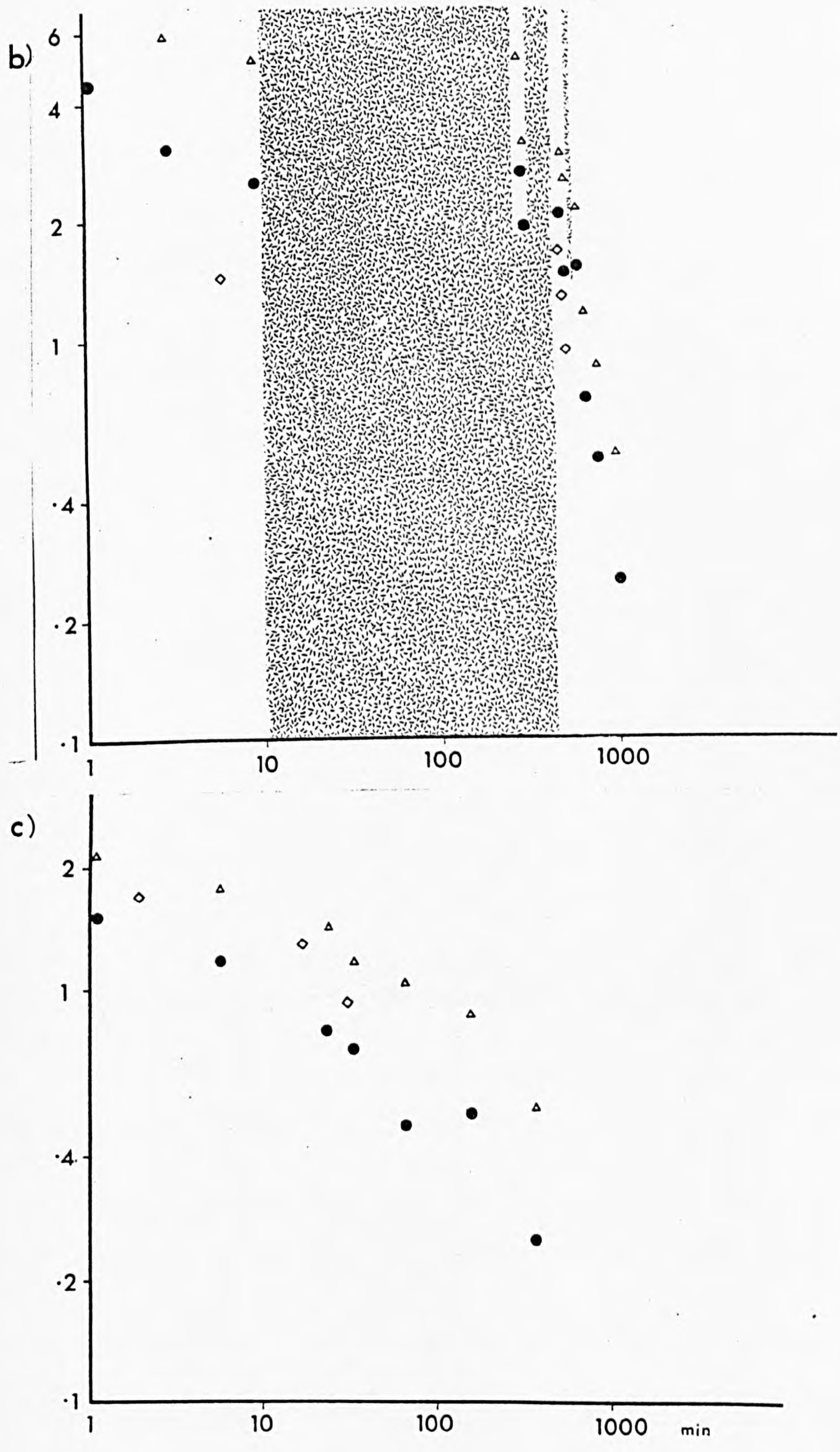


Figure 10 The decay course of McCollough aftereffects induced shortly before a night's sleep, plotted on a) linear/linear coordinates, b) log/log coordinates with time origin at the end of the McCollough exposure, c) log/log coordinates with time origin at the opening of the eyes on the second day.

- ● VM left eye 12 min exposure) ending 11.18 p.m. 24 May, 1974.
- △ VM right eye 37 min exposure
- ◇ DMM both eyes 22 May, 1974.

The dotted line in figure a) shows the decay, in the light, of an effect induced by a similar 12 min exposure of VM's right eye ending at 12.48 p.m. on 6 November 1973 (figure 9).
Sleep occurred during the parts of the graphs shown dashed in a) and speckled in (b). Vertical bars show the scatter (twice the standard error) of the last mean reading of each group.


b)
6
4
2
1
·4
·2
·1
1
10
100
1000
c)
2
1
·4
·2
·1
1
10
100
1000
min

replotted with time origin at the time of opening the eyes in the light at the start of the second day.*

Findings: In almost every case the first readings immediately after a period of sleep are as high or even higher than the last readings before it. During each 8 min period of taking readings following sleep, the readings fall very rapidly after the manner of a newly induced effect. Even so the last readings in each group are 3 or 4 times above the level of the comparison run at the same time after the McCollough exposure. The course of decay in the light on the second day is highly similar to that of the comparison run at times 10 hours earlier (figure 10(a) and (c)). Log/log plots with the time zero moved by this amount to the time of waking on the second day (figure 10(c)) have slopes similar to those of newly induced effects.

Subjectively the test figure was quite stunningly colourful especially for the right eye throughout the two periods of viewing it 5 and 8 hours after induction. During the first period the hues were judged to be just as strong as before going to bed.

The subject found the (0.5 log ft L, i.e. 11 cd/m^2) test field almost distressingly bright for the first 1½ min after each awakening, but after a further ½ min felt that vision was normal.

Conclusion: During sleep and darkness the McCollough effect does not decay in the same manner as in the normal daytime environment. During 5 hours in

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* In figure 10(c) DMM's readings are multiplied by a constant factor.

the dark decay was near zero, whereas during a similar period in the light the aftereffect falls to below a quarter of its initial strength.

5.3.1.1 Dark Adaptation: an influence on hue matching?

Keith White (1976, p. 36) has pointed out that since dark adaptation will reduce the subject's sensitivity to the colours presented by the colour mixer (Lie, 1963, p. 481; Stabell and Stabell, 1975), spuriously high readings can be expected for some minutes after a period in the dark. This criticism can hardly be applied to the arrowed readings in figure 9 since they were made some two hours after waking. It is unlikely that it seriously affects the (bracketed) last readings of each group in figure 9 for these were made after 7-8 min* in the light. But such a factor may influence the earlier readings and so is investigated in the following control experiments.

5.3.1.2 To assess the influence of dark adaptation upon the making of hue matches

Two experiments were performed. In the first, a 20 min dark period followed the McCollough exposure immediately; in the second, a period in the light preceded a dark period of 15-45 min.

5.3.1.2.1 Matching the hues of a large McCollough effect recently induced

The left eye was exposed to McCollough stimuli for 20 min, the right

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* Lie's (1963) graphs show a time constant of about 1½ min for the alteration of the photochromatic interval during dark adaptation. I am assuming a similar time constant holds for readjustment to mesopic light levels. The results of Rushton and Gubisch (1966) which show recovery from, as well as adaptation to, darkness suggest that equal time constants (of about a minute at most) apply to the two processes.

eye being covered; then the left eye was kept in total darkness for 20 min while the right eye was given an identical McCollough exposure. The subject then viewed for 1½ min a white card at 0.5 log ft L before making hue matches alternately to the aftereffects in the two eyes. The readings taken on the two eyes between 1½ and 6 min after the end of the left eye's 20 min period of darkness are given in table 6.

Table 6 Readings of the aftereffects in the two eyes after identical McCollough exposures. The left eye had been dark adapted for 20 min and the right had not.

VM 25.3.77	Left	Right
	4.45	5.75
	4.10	4.25
	3.30	3.20
	2.30	3.05
	2.35	2.50

Findings: There is no significant elevation of the readings made using the dark adapted (left) eye relative to those made with the other eye. Subjectively also the McCollough effects seen by the two eyes were highly similar.

5.3.1.2.2 Matching the hues of a McCollough effect which had been decaying for a day

A moderately large McCollough effect was allowed to decay in the light for 10 hours. The subject then sat in darkness starting at 9 p.m. for 15, 45 min respectively on two different occasions. Hue matches were performed immediately before and after the period of darkness. The readings were in each case raised by 50% for the first reading - from 0.7 before the dark period to an average of 1.0 during the first minute after it.

But the readings fell very rapidly and returned to their former level within 3.5 min. The subject felt the appearance of the aftereffect was not altered by the 15 min in darkness, but that the aftereffect was 'clearer' and 'possibly stronger' after the 45 min rest.

Findings (experiments 5.3.1.2.1 and 5.3.1.2.2): The hue matches were not elevated by a period of darkness in the first experiment and yet were elevated in the second.

Discussion: The main difference between the two situations would seem to be that decay in the light had occurred prior to the period of dark adaptation in the second experiment but not in the first. The fact that the readings are elevated in the second case therefore seems to be ascribable not so much to the effects of dark adaptation upon hue perception as to a recuperation of the McCollough effect in darkness. (See also 5.5.1.)

5.3.1.2.3 Conclusion

One to 3 minutes after a period spent in darkness, the effects of dark adaptation have a negligible effect upon the judgement of hues.

The fact that readings are - even slightly and for a short time - affected by darkness imposes regrettable but unavoidable limits upon the certainty with which the amount of decay can be determined from the first readings following a period under dark or dim conditions. It is for this reason that later experiments concentrate upon the readings long after the effects of the dark period will have worn off.

5.3.1.3 Conclusion: The effects of sleep and darkness

Returning to the gap between the two graphs of figure 10a at 10 hours, nearly half the gap is left still unaccounted for when the effects of darkness revealed by the control experiment 5.3.2.2 above have been allowed for. There can be no doubt then, on the basis of figure 10a (and later experiments show this even more clearly), that decay of the McCollough effect does not proceed as fast in sleep and darkness as when light is entering the eye. Later experiments investigate whether or not decay is totally arrested in darkness (5.4.2, 5.5).

The object of experiment 5.3.1 was to find out why the arrowed points on figure 9 are as high as they are. The principal reason seems to be that the McCollough effect suffers considerably less decay when the subject is asleep than in the day time. It is possible also that a slight re-cuperation of the McCollough effect from earlier decay occurs in darkness.*

The fact that the arrowed points are actually above the level of the previous evening's readings cannot be ascribed to the effects of dark adaptation on the making of hue matches since these arrowed readings were made two hours after waking. Dark adaptation probably elevates the readings for at most 3-5 min after opening the eyes.

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* For further instances of elevated readings, see figures 13 and 18 of sections 5.3.6.1, 5.5.1.

The preceding experiment (5.3.1) had shown that sleep and/or darkness reduce the rate of decay of the McCollough effect considerably and perhaps totally. The next experiment investigates whether absence of light, absence of patterned light or sleep was the necessary condition for arrest of decay.

5.3.2 <u>To compare the decay of the McCollough effect in the normal environment with that in darkness and by unpatterned illumination</u>

<u>Apparatus</u>: The pre- and post-exposure measurements were made using apparatus M_1 with test card T_2 at 65 cm. The oblique orthogonal red and green McCollough stimuli of 2.2 cycles/degree were presented by the two projectors with shutter (E_1), with a timing cycle of 6 sec on, 3 sec off and viewed binocularly for 20 min.

<u>Experiment 5.3.2.1</u> <u>Darkness versus the normal environment</u>

Immediately after making the four post exposure settings on each eye a light-tight patch was fixed with black plastic adhesive tape across the eye socket of the subject's left eye. The subject then spent 6 hours in ordinary activities by daylight before the patch was rapidly removed and hue settings were made using the two eyes alternately. Further readings were made over the next hour.

<u>Results</u>: Figure 11a shows, on log/log coordinates the readings made using the two eyes. The time origin is at the end of the McCollough exposure. Figure 11d shows the results for the eye which had been covered, plotted on log/log coordinates but with time origin at the removal of the black patch.

Figure 11c shows the results of a control run in which, following a 10 min McCollough exposure, both eyes were exposed to the normal environment for 96 min.

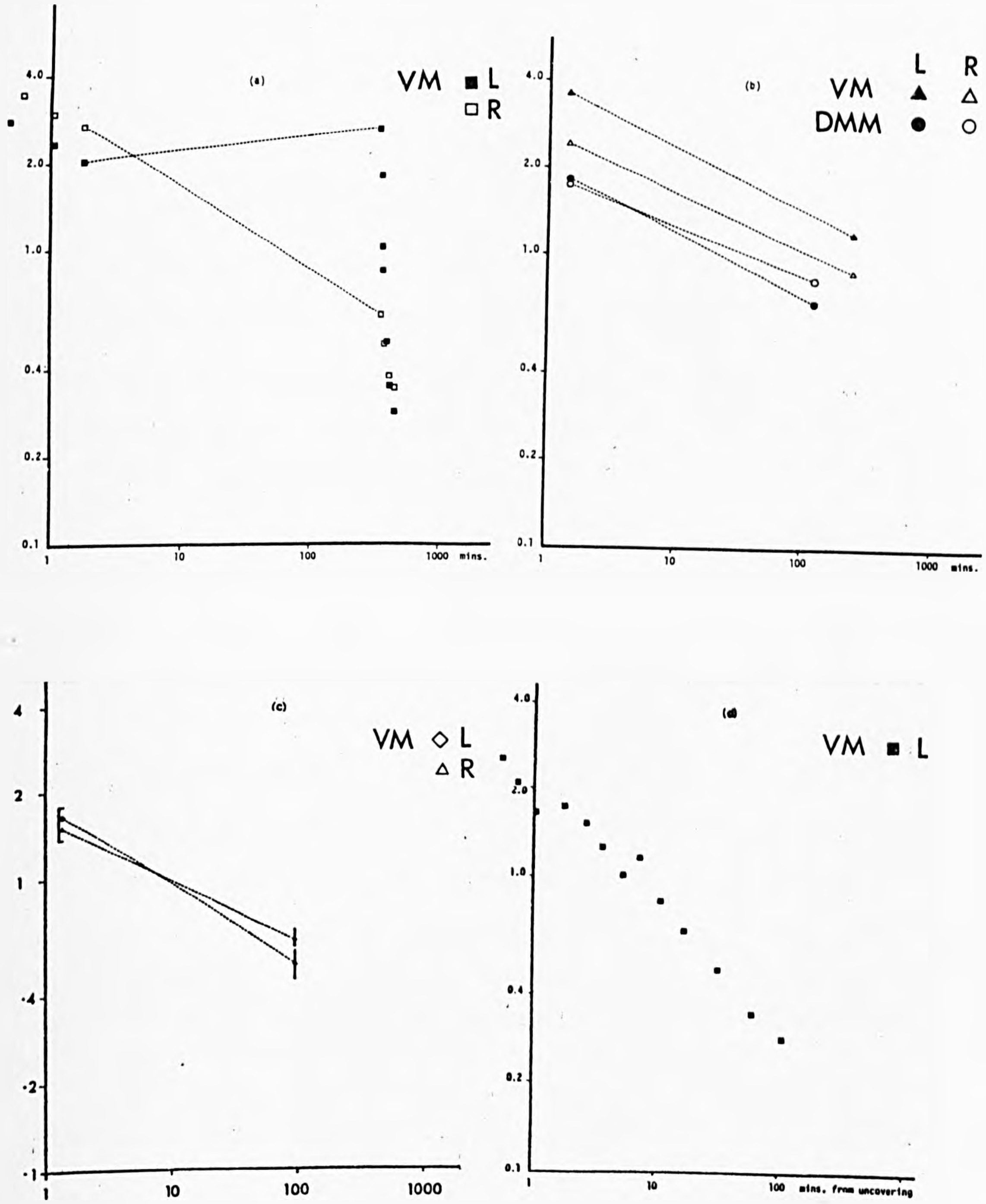

Figure 11: Comparison of the effects of the ordinary environment (open symbols) with that of (a) darkness, (b) diffuse illumination, on the time course of the McCollough effect (c) control run: decay in the ordinary environment. Error bars show twice the standard deviation. (d) The later readings on the covered (left eye) of figure 11a replotted on log/log coordinates with time origin at removal of the black patch.

Findings: Upon removal of the light-tight patch the readings show a distinct difference (x 4) between the strengths of the aftereffects in the two eyes. A significant difference persisted for 17 min. After the patch had been removed, decay followed the type of course which we have already noticed following a night's sleep (experiment 5.3.1). On a log/log plot with time origin at the end of the McCollough exposure, the decay following removal of the black patch is very steep (figure 11a), but if a new time origin at the end of the period of darkness is used, the decay slope is similar to that observed when induction of a McCollough exposure is followed by admission of light to the eye (figure 11d). This phenomenon is investigated in experiment 5.5.

Conclusion: This experiment shows that sleep was not an essential feature for producing the arrest of decay in experiment 5.3.1.

Experiment 5.3.2.2 Unpatterned stimulation versus normal environment

Immediately after making the four post exposure hue matches a fine uniform tissue (Chartwell gateway tracing paper) was stuck with tape across the eye socket of the subject's left eye. The grain of the paper was not visible at this distance from the eye and no contours were visible through it (though there was a shallow gradient of intensity towards the room's windows). The paper dimmed the light by a factor of two.

After a few hours spent in ordinary activities by daylight (at about 1.1 log ft Lamberts) the paper was rapidly removed and hue settings were made monocularly on the two eyes.

Results: Figure 11b shows the readings for the two eyes for two subjects before and after the tissue was affixed. For DMM the interval was 2 hours, for VM 4 hours.

There is no significant difference between the rates of decay in the two eyes of each subject.

Conclusion: Unpatterned light produces as large a decay of the McCollough effect as the normal environment. Further experiments in which decay occurs in an unpatterned environment are described in 5.6.

5.3.2.3 Discussion: The use of one eye as a control

The practice of using one eye as a control for an experiment which is proceeding simultaneously in the other eye needs justification.

We have already seen (experiment 5.1, Table 3) that the rate of decay in each eye was, to a first approximation at least, independent of the aftereffects in the other eye. Experiment 6.3.1 supports this impression. It also reveals, however, that there is a considerable (25%) binocular element in the McCollough effect. But since this element seems to be undetectable except by binocular testing I assume that its presence does not affect the results obtained by the monocular testing at present under discussion. Transfer of the McCollough effect from one eye to the other monocular channel is below 10% (experiment 6.2.1).

A comparison (see figure 11) of the decay which took place during exposure to the normal environment under monocular (figure 11a and b) and binocular (figure 11d) conditions suggests that a simultaneous control run performed in the other eye is about equivalent to a control run on another day. It is probably, indeed, more reliable since the metabolism will be more similar for the two eyes.

Experiments were next performed to find whether decay was hastened by exposure to an environment rich in edges. Only one of these is described in detail, the rest are summarised below.

5.3.3 Decay of the McCollough effect in a strongly patterned environment

If subjects with a McCollough aftereffect view a test field continuously at usual luminance levels (1.7 log ft L) the illusory hues fade completely within 5-20 min. I have performed several experiments to investigate this acceleration of decay by exposing one eye (after binocular McCollough exposure) to achromatic gratings with white stripes at 1.7 log ft L and the other to an unpatterned field of the same average luminance. After 10-20 min, the decrease which had occurred in S, the difference between the hue settings, was about 40% greater for the eye which had viewed the grating(s). The largest rate of decay was produced by chromatic gratings parallel to the gratings which had been used to induce the effect. These binocular experiments were discontinued because it seemed impossible to devise a neat control in which space average luminance and local luminance of the light bars could be matched in the two eyes and also because I heard that Diane Skowbo was about to publish similar conclusions.

Skowbo, Gentry, Timney and Morant (1974) gave 10 min McCollough exposures to three subjects and compared the decay which occurred - on different occasions - during 50 min spent in viewing i) achromatic gratings, ii) homogeneous coloured fields, and iii) the 'natural' indoor and outdoor environment. (Each 50 min period was followed by a further 7-12 min spent in viewing homogeneous fields, before the measurements were made.) Decay was two to four times greater when exposure was to the achromatic gratings than for the other conditions.

The technique developed in chapter eight, for measuring the chromatic aftereffect separately at any orientation, later offered a useful way of exploring the effect of an achromatic grating on decay. It made it possible in effect to perform experiment and control simultaneously in one eye. Below is a pilot run using this technique.

Experiment 5.3.3.1 To investigate the effect upon the decay of the McCollough aftereffect of continuous exposure to an achromatic grating

The apparatus and procedure were identical with those described for experiment 8.1.1 (on the induction of multiple orientation-contingent aftereffects) to which this experiment in fact formed a sequel.

Apparatus E_3 was used to present six gratings at six orientations at 30^o to each other in red and green light for a total of one hour.

After the subject had rested for 10 min in darkness, test apparatus M_2 was used to measure the resulting aftereffects at orientations about 5^o apart (figure 12; 3.38-3.45 p.m.). The solid and dotted bars indicate the orientations at which red and green gratings respectively were presented. Green aftereffects are plotted upwards. The abscissa shows the orientation of the test grating T_1 (inset below). Displacements of the plotter pen which correspond to green orientation-contingent aftereffects are plotted upwards (scale in cm). Then, for 12 min (3.46-3.58 p.m.) the subject viewed continuously, though without fixation, an achromatic horizontal grating (of luminance 24 cd/m^2 on its white stripes and 2 log units contrast). Its spacing was identical with that of the gratings used to induce the chromatic aftereffects.

Twelve minutes' rest in darkness followed.* Then the subject made

* This dark period was introduced because it had been noticed in the earlier experiments that the test gratings were temporarily much less sharply visible (cf. Blakemore and Campbell, 1969b) when their orientation was the same as that of the achromatic grating, and that this impairment of visibility wore off after about 3 min spent in the light or in darkness. Since the McCollough effect was known to be little affected by darkness, (experiment 5.3.2.1; MacKay and MacKay, 1975b) it seemed a good policy to separate the various factors by waiting for a few minutes in darkness.

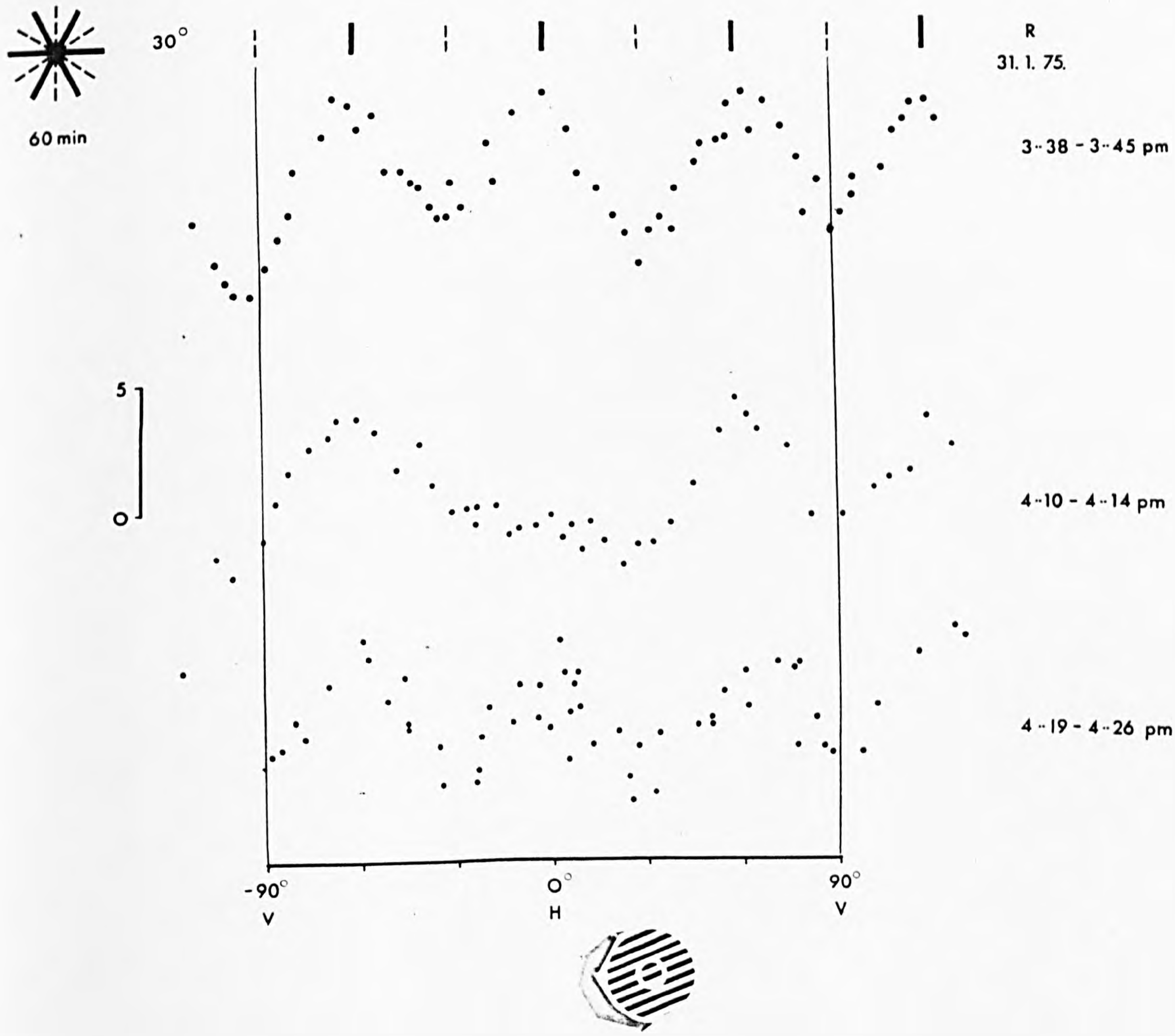

Figure 12

The temporary reduction of the McCollough aftereffect at the horizontal orientation, produced by viewing a horizontal achromatic grating for 12 min (4.10-4.14 p.m.).

hue matches in the usual manner progressing clockwise and later anti-clockwise by steps of about 5°. After half a minute at normal room illumination, further hue matches were performed with the test grating orientations presented in random order (with a view to randomising the effects of chromatic adaptation on the subject's hue settings).

Results: Figure 12 shows the angular distribution of the aftereffects before and after exposure to the horizontal achromatic grating (at 3.46 -3.58 p.m.).

On the clockwise traverse at 4.09-4.13 p.m. the test grating appeared colourless when it was within 30° of the horizontal. On the anti-clockwise traverse, however, (4.14-4.18 p.m.)a pink hue was noticeable on the test grating when it was horizontal. And by the time the hue matches were made in random order (4.19-4.26 p.m.), the hue seen on the grating when it was horizontal was comparable with that seen when it was tilted by 60° to either side.

The measurements show a temporary elimination of the chromatic aftereffect near the horizontal and subsequent recovery to above 50% of the strength at the adjacent maxima. This recovery took place within the 27 min since the end of exposure to the achromatic grating, and probably - since the aftereffect was so little visible at 3.09-3.13 p.m. - during the 10 min of exposure to the dimly lit test card.

Conclusion: When an achromatic grating is viewed continuously for a few minutes, pre-existing McCollough aftereffects within about 30° of the grating's orientation are rendered temporarily invisible. Appreciable recovery occurs within ten minutes of subsequent exposure to light.

5.3.3.2 Discussion: The recovery of a McCollough aftereffect from the reduction in saturation which is produced by viewing an achromatic grating

Graves (1976)* and also Skowbo and Clynes (1977) have independently found spontaneous recovery. In

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* As reported by Keith White (1976, pp. 32, 80).

Skowbo et al's paper (1974) the difference between the amounts of decay produced by the achromatic grating in experiments I and II also invites interpretation in terms of a recovery which takes place while viewing the 'homogeneous fields'. For it is the interrupted exposure to the achromatic grating (experiment I) which produces the smaller drop in aftereffect strength (in spite of the fact that the total interval between first and last reading is 23 min longer than in experiment II).

The next question is whether these effects of an achromatic grating - viz. accelerated decay with subsequent recovery - are the result of a fresh superimposed McCollough exposure or of some other aftereffect induced by the achromatic grating. Keith White (1976, p. 80) with Graves reports tentatively the interesting discovery that 'prolonged viewing of achromatic gratings may reduce the apparent saturation of chromatic gratings' in the absence of a McCollough effect. Graves (see White, 1976, p. 32) has also found that the magnitude of the reduction of the McCollough effect by a given period of viewing of achromatic gratings is nearly 'independent' of the extent to which the McCollough effect has been allowed to decay before the achromatic gratings are viewed. White and Graves therefore incline to the view that the reduction of the McCollough effect may be the result of 'a desaturating influence entirely independent of . . . contingent after effects' (White, 1976, p. 8). The fact that in experiment 5.3.3.1 recovery occurred rapidly once light was admitted to the eye though not during the preceding 10 min of darkness is perhaps a useful clue towards the identification of this 'influence'.

5.3.4 <u>The making of measurements as an influence on the rate of decay of the McCollough effect</u>

The fact that viewing an achromatic test card reduces the magnitude of the observed McCollough effect revives the question already raised in chapter 4.4.2.4, as to how far the procedures of measurement themselves affect what is to be measured. In our apparatus the subject views not only an achromatic field which will presumably reduce the effect (5.2.3), but also, foveally, a $5.6^{o} \times 1.9^{o}$ area of tinted stripes which will act as a fresh McCollough stimulus with a nett tendency to increase the subject's McCollough aftereffect.

Taking the decay course as a whole, the nett effect of a moderate amount of measurement seems to be small* (see below, 5.2.4.3), but the maximum disturbances that can be produced by the above two factors must first be considered.

5.3.4.1 Rapid local decline of readings

Groups of measurements often show a feature which suggests that testing does affect the measurements, if only temporarily, within a group of three or more readings, involving 1-3 min viewing of the test field, the readings often fall at a rate much more rapid than the average rate of decay of the graph. Thus, for example 10-20 min after the McCollough exposure, the local fall within each 2 min group of readings may be 10%, and this equals the overall drop over the ten minute period. When a new group of readings is started the reading has generally recovered and is slightly above the last readings of the preceding group. Such recovery occurs within as little as 2 min. This pattern of decline and recovery can be seen in the first four groups of readings of figure 3b, and throughout figure 28 a, b and c. In figure 28 b and c there is no averaging of the raw readings for the first 9, 1000 min respectively. The 20% spread of the readings about the mean decay course is not produced so much by random variations as by this systematic decline of the readings

* This is the case at ordinary luminances of 1.0 log ft L upwards. At lower luminances decay differs considerably according as some or no readings are performed (see 5.4.4).

during each group of measurements. When a long group (of 8 or more) readings is taken the decline does not continue indefinitely but is largely complete within about 2 min i.e. within the first two or three readings (cf. figure 3a, b - the last group of readings in each). The absolute magnitude of this effect is greatest when the McCollough effect is large, but as a fraction of the McCollough effect it remains roughly constant (cf. figure 28 a, b c). The times (about 2 min) which this effect takes to reach saturation and to recover are reminiscent of those described by Blakemore and Campbell (1969a, b) for the reduction in visibility of gratings. But the possibility that the phenomenon is to some extent a property of the McCollough mechanism remains open.(9.3.1)

<u>Summary</u>: The making of readings using our test apparatus brings about a 10% decline of the readings in the course of 2 min of readings, but most of this decline is only temporary.

5.3.4.2 <u>The effect upon the subject's McCollough aftereffect of viewing coloured gratings in making the hue matches</u>

Unsaturated colours are quite effective McCollough stimuli; an exposure to gratings in which the usual red and green filters were replaced by 'rose pink' and 'pale green' (Cinemoid 54, 2 layers; and 38, 1 layer respectively) produced aftereffects only one third less strong in the same time. In our apparatus the $5^{\circ} \times 2^{\circ}$ windows of the test figure take on saturations which closely match these cinemoid filters when the knob is turned to positions corresponding to a reading of S =˜ 2cm. I have therefore simulated a 2 min period of making readings, in which the colour mixer is turned to such settings, and have measured the McCollough effect which this exposure to the test field induces in initially unbiassed eyes. The average effect induced in several 2 min sessions had an initial strength of S = 0.05 cm. This is so small as to be invisible, but it makes a just detectable shift in the hue match settings for 1 or 2 minutes.

To gain an idea of the upper limit to the effect which the coloured windows could exert upon readings, an 8 min simulated session was also performed in which the colour mixer was turned repeatedly to its two maxima (this would correspond to an effect of $S \doteqdot 6$ cm). The resulting aftereffects had an initial magnitude of $S = 0.3 \pm 0.05$ and took 30 min to disappear. In practice such strong hues have never been viewed for even half this length of time.

Conclusion: The viewing of the coloured windows of our test figure for 2 minutes of making measurements increases the effect to be measured for 1-2 min by at most 2%

As a systematic rise in the readings is never in fact observed (see 5.3.4.1), the above increase in McCollough effect is presumably concealed by larger factors making for a decline of the readings.

5.2.4.3 Does measurement affect the overall form of the decay curve?

Several runs have been performed with the minimum of measurement, for comparison with those in which a large number of readings were taken. Three runs involving very little measurement are shown in figures 3a and 4a, the upper graph of figure 9, and figure 11d. The values of β for these runs (-0.29, -0.26, -0.22 and -0.30 respectively) are not noticeably different from those of runs in which many more readings were taken.

Summary: The effects of exposure to the achromatic and the coloured gratings of our test card are short-lived and are such as to partially cancel each other. A moderate amount of measurement is without significant effect* on the overall course of decay of the McCollough effect. (See also 5.6).

5.3.5 The colour of light entering eye during decay

It seemed possible that the rate of decay of the McCollough aftereffect might differ according as the same or different cone systems were principally excited during induction and during decay. Red and green interference filters were worn on the two eyes for some four hours following binocular exposure to a red or to a green grating. Small differences in decay rate were found but it seemed probable that these were attributable to the different degree of attenuation by the filters. So in subsequent experiments an interference filter was worn on one eye while the other was covered by a neutral filter of matching attenuation. No significant difference was found between the decay in the two eyes, but it was noticeable that decay was slower when dimmer filters were worn. This phenomenon is further investigated in experiment 5.4.4.

Conclusion: The colour of the light viewed during decay makes no obvious difference to the rate of decay of the McCollough effect.

In view of the very broad spectral sensitivity of the cones this result was probably to have been expected.

5.3.6 The state of the subject

5.3.6.1 Chemical intake

It is noticeable that the measurements of the McCollough effect during decay (and of the initial aftereffect on different days) suffer quite large (15%) fluctuations. Some, at least, of the fluctuations during decay appeared to be uncorrelated with the subject's recent visual diet,

* See, however, footnote to 5.3.4.

and we have been inclined to attribute them to metabolic variations. For example, we have quite often found, when tired in the evening, that a cup of sweetened Nescafé seemed to produce a noticeable increase in the colourfulness of a faded aftereffect. Figure 13 shows, arrowed, the readings on one such occasion, made 8 min after drinking the coffee. The suggestion that the McCollough effect results from modifications in synaptic connectivities (MacKay and MacKay, 1974a, 1975b) leads one indeed to expect that drugs which are held to affect synapses will affect the aftereffect. The problem, however, even in the case of a weak drug like the Nescafé above, is to know how much of the alteration in the aftereffect is ascribable to the effects of the drug on the McCollough mechanism itself and how much is ascribable to the effects of the drug on the many other parts of the subject's visual and perceptual system* which are processing the signals from the achromatic test card.

One type of experiment** would therefore consist in monitoring some other visual skills besides the McCollough effect while the subject is under the influence of the drug to see whether the McCollough effect is affected more than those other parameters (e.g. visual acuity and the perception of pale colours) which are involved in the judgement of McCollough aftereffect strength.

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* As subjects in experiments by my husband (1976 unpublished), Keith Bradshaw and I have both found that drugs such as hyocine and ephedrine severely affect ones carefulness in hue matching, ones ability to focus well and even ones power of keeping awake and the eyes open!

** Not yet performed so far as I am aware.

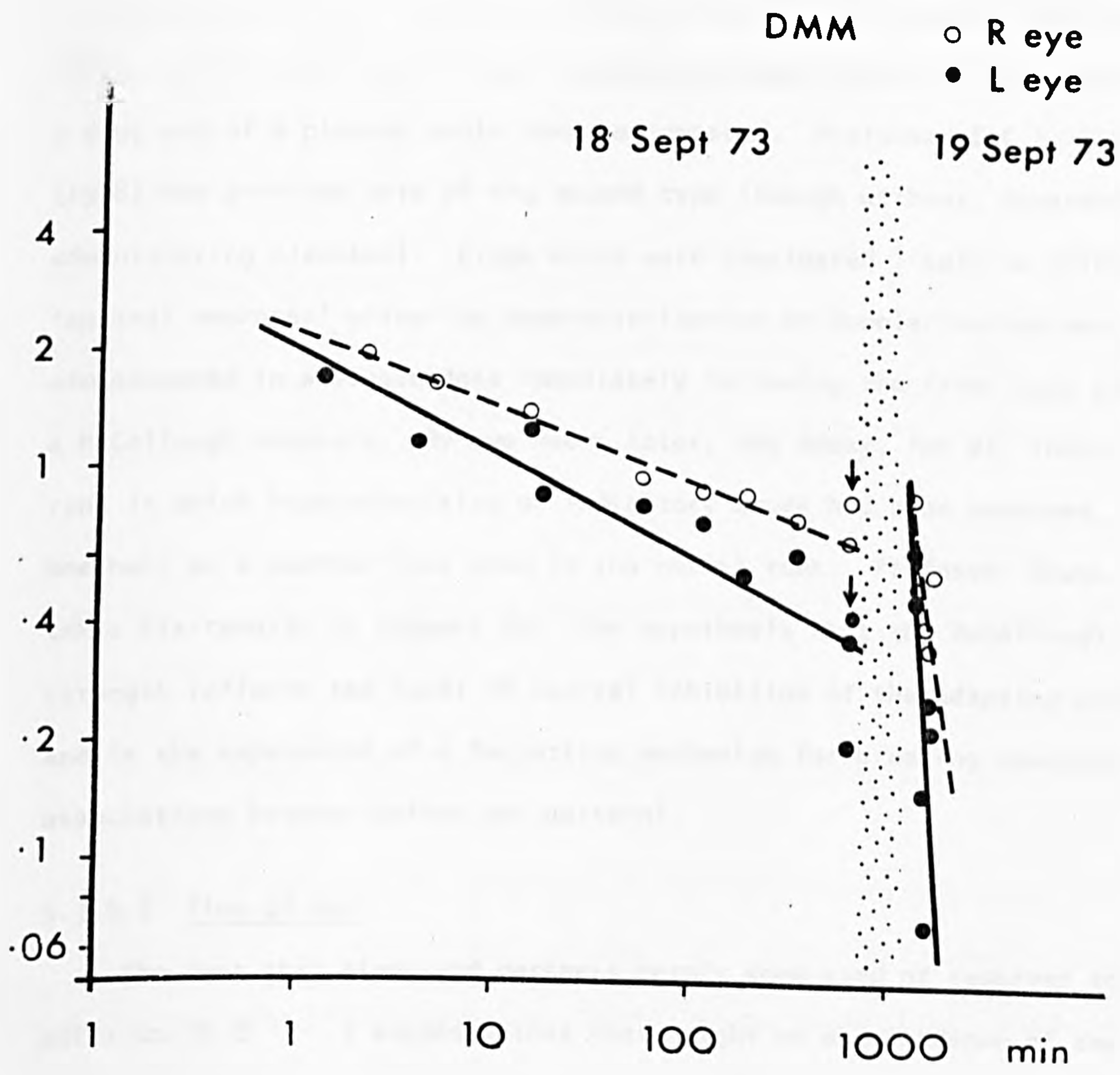

Figure 13 Factors affecting the decay of the McCollough effect

The arrowed readings were made 8 min after drinking a cup of sweetened Nescafé.

Note incidentally the even greater elevation of readings at 9.25 am after a night's sleep (speckled).

Another type of experiment would be to make all measurements when the subject is in as nearly as possible a normal state, i.e. before consumption of the drug and after its effects have worn off. The decay of the McCollough effect which takes place in the intervening hours under the influence of a drug and of a placebo could then be compared. Professor C.C.D. Shute (1978) has provided data of the second type (though without, apparently, administering placebos). Drugs which were considered likely to affect 'central neurones' either by hyperpolarisation or depolarisation were administered in a single dose immediately following the first test after a McCollough exposure. By two hours later, the decay, for all those runs in which hyperpolarising or inhibitory drugs had been consumed, was one half or a quarter less than in the normal runs. Professor Shute takes his results as support for 'the hypothesis that the McCollough effect strength reflects the level of central inhibition of the adapting colour and is the expression of a forgetting mechanism for breaking unwanted associations between colour and pattern'.

5.3.6.2 Time of day

The fact that sleep and darkness permit some kind of reserves to be built up (5.5) suggests that there might be a dependence of the initial strength or of the subsequent decay rate of a newly induced effect upon the time of day at which the McCollough exposure takes place. Both factors unfortunately show considerable random variation (up to 20%). Table 6 shows the values of β for two subjects following exposures at different times of day but under otherwise identical conditions.

The trend towards slower rates of decay cannot be ascribed with certainty to the subject's internal state, since not all factors (in particular the ambient level of illumination) were controlled.

Table 6: Variation of rate of decay with time of day

DMM: Right eye exposed 20 min.

Time	Date	β
9.47 a.m.	1 May 1973	-0.19
12.20 p.m.	13 August 1973	-0.15
3.24 p.m.	30 April 1973	-0.12

VM: Binocular exposure, 10 min.

Time	Date	β
9.56 a.m.	2 April 1977	-0.23
9.06 p.m.	16 January 1975	-0.18

Conclusion: The decline of the rate of decay as the day proceeds is not above 30%.

5.3.7 Summary: Factors influencing the rate of decay of the McCollough effect

Decay of the McCollough effect is not spontaneous but depends for each eye upon the visual input to that eye. Light, patterned or unpatterned seems to be the essential factor for bringing about recovery from the McCollough aftereffect, for no decay occurs in darkness and appreciable decay occurs with diffuse illumination. The patterning of the visual stimulus is, however, not without significance, for accelerated decay is brought about by exposure to achromatic gratings whose orientations are similar to those of the inducing gratings.

The subject's physiological state possibly affects the rate of decay.

5.4 The influence of darkness and of other levels of illumination on the decay of the McCollough aftereffect

Of the above factors which influence the rate of decay of the McCollough effect the most potentially informative is the amount of light entering the eye. We shall consider this aspect more closely in sections 5.4 and 5.5, dealing first with the question as to whether a small decay, or none at all, takes place in darkness. In the experiments so far (5.3.1) a maximum of 5 hours was spent in continuous darkness. In order to give a small decay a better chance to reveal itself the dark period was extended.

Experiment 5.4.1 Decay of the McCollough aftereffect in an eye from which light was excluded for 24 hours

5.4.1.1 Simultaneous induction in control eye*

Apparatus: The pre and post exposure measurements were made using test apparatus M_1 with test figure T_2 at 67 cm. Oblique red and green gratings of 2.2 cycles/degree were presented binocularly by the two projectors with shutter (E_1), for 20 min, with a presentation cycle of 6 sec on, 3 sec off.

Method: Immediately after the end of the McCollough exposure the subject made four pairs of hue match settings with each eye (used alternately) and then, the room being still in darkness and with the right eye closed, a light tight black patch of several layers of black card and black plastic tape was stuck to areas of black tape on the face which had been prepared beforehand. The room lights were turned on and leaks in the

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* Experiments 5.4.1.1 and 5.4.1.2 were published in MacKay and MacKay (1977a, 1978).

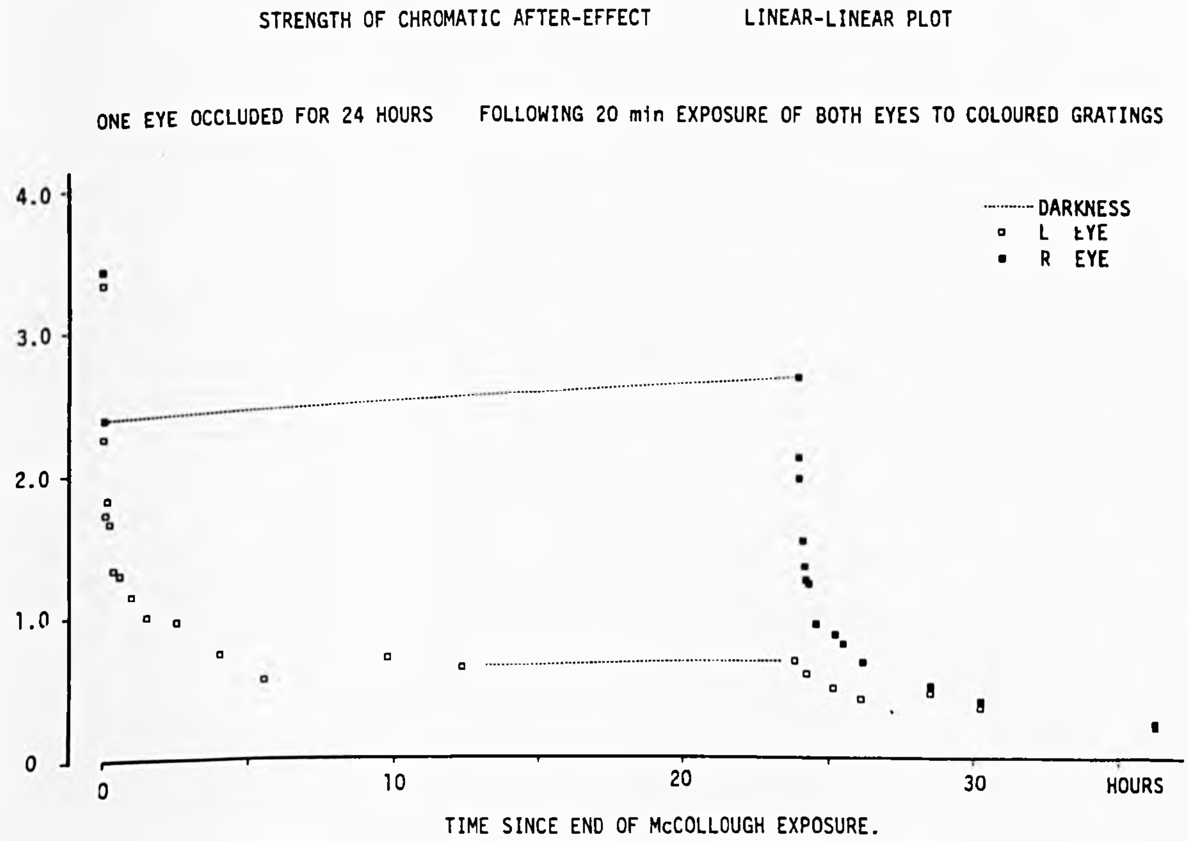

Figure 14

Showing the retention of the PCCA in a subject's right eye, occluded for 24 hours after exposure (■) compared with that in the left eye, exposed for the same time to a normal environment (□). Periods in darkness, for each eye, are shown by dotted lines.

black patch sealed as they became visible. Further readings on the left eye were made at intervals until the following morning.

Twenty-four hours after it had been put on, the patch was removed from the right eye, the subject faced the test field, opened the right eye and commenced measurements using it. Ordinary life and further measurements on both eyes at intervals were continued through the second day.

Results: Figure 14 shows the measurements on each eye as functions of the time in hours from the end of the first exposure.

No detectable decay of the McCollough effect in the right eye occurred during the twenty-four hours in darkness. The subject considered that the hues seen when the patch was removed looked as saturated as they had done immediately after the McCollough exposure. The hue match settings were if anything above those made before the patch was put on. The readings for this eye were then four times as large as those on the eye which had been receiving light normally through the previous day. One and a half hours later (long after the effects of dark adaptation had worn off) the McCollough effect seen by the right eye was still about twice as strong as that in the left eye.

For many hours after removal of the black patch, the form of the decay course of the 'covered' (right) eye's effect was similar to that observed in the left eye on the preceding day.

Summary: The McCollough aftereffect suffers little or no decay in an eye from which light is excluded.

Although the decay courses of the aftereffects in left and right eyes in the previous experiment were closely similar, they were not completely identical. It is possible that the second day's aftereffect decayed more rapidly because the day was sunnier, or the subject's metabolic state was different or because there is a binocular component to the McCollough effect which could decay only when the two eyes were simultaneously in use. On the other hand the difference in decay rate might indicate that the McCollough mechanism had been undergoing changes during the twenty-four hours in darkness which enabled it to fade faster once light entered the eye again.

The next experiment seeks to separate these two possibilities by arranging that conditions of lighting and metabolism should be identical for the two eyes throughout decay.

Experiment 5.4.1 Decay of the McCollough aftereffect in an eye from which light was excluded

5.4.1.2 Simultaneous decay in control eye

Apparatus and Method: The pre and post exposure measurements were made using apparatus M_1 with test figure T_2 at 67 cm. On the first day, oblique orthogonal red and green gratings were presented monocularly, (the other eye being closely covered) using two projectors (E_1) and the presentation cycle of 6 sec on 3 sec off. Immediately following the exposure one min was spent in making 4-5 pairs of readings on this exposed eye before it was covered by a light tight black goggle sealed to the face by black plastic tape. The next morning, 12½ to 25 hours later, the other eye was given a McCollough exposure identical in every respect to that of the preceding day. This was followed by 1 min spent in making 4-5 readings on the newly induced effect. The subject then sat in darkness with both eyes closed for 2½ min-4min while the black patch was removed. Readings on the two eyes alternately were then commenced.

DECAY OF CHROMATIC AFTER-EFFECT IN THE TWO EYES
UNDER IDENTICAL CONDITIONS OF LIGHTING AND METABOLISM

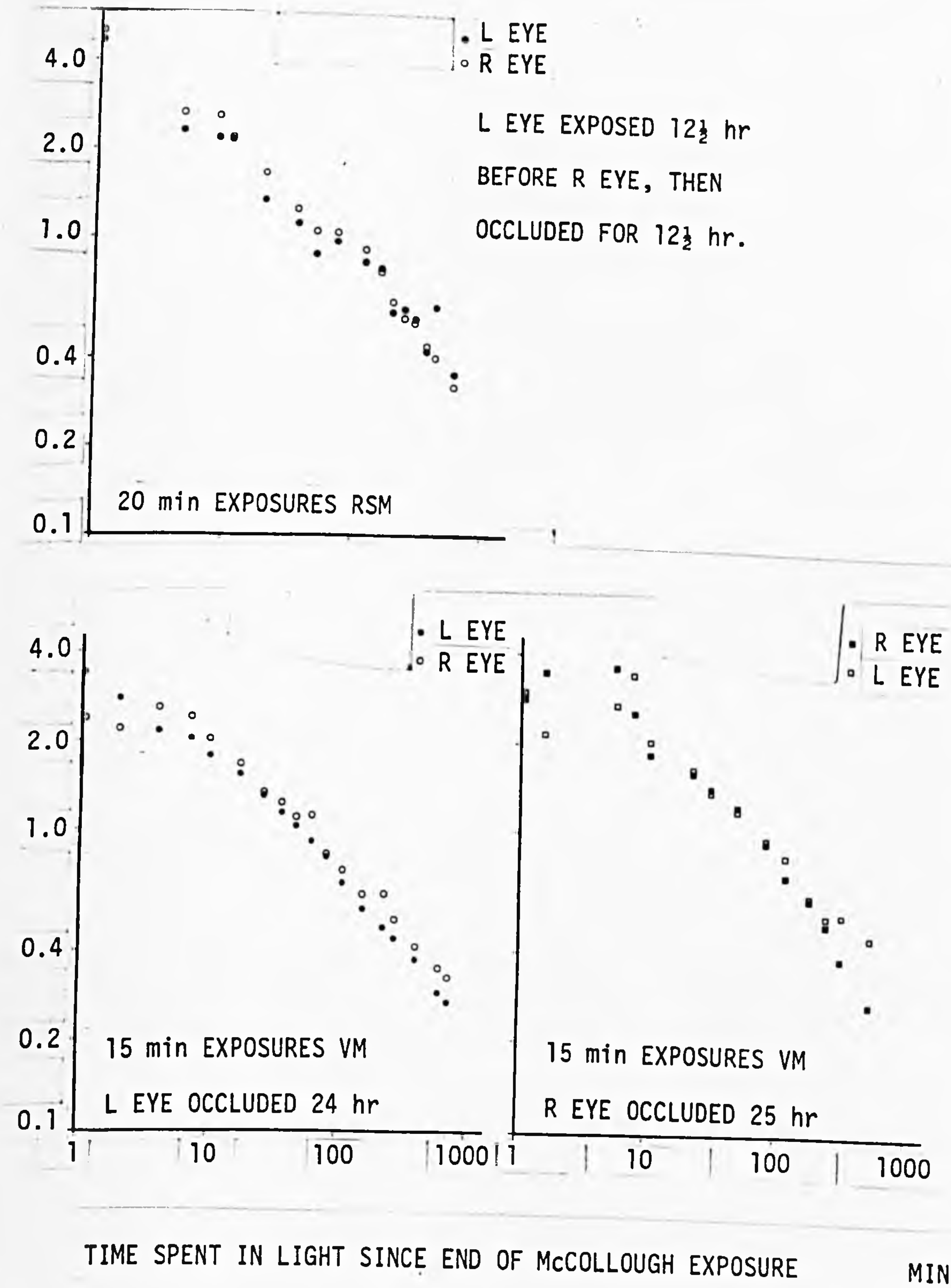

Figure 15

Three runs on two subjects showing how similar are the magnitudes and decay-slopes of the PCCA for an eye exposed to the McCollough stimulus and then kept covered for 12½ to 25 hours, to those for the control eye freshly exposed.

The subjects remained in one room lit at 1.1 log ft L for most of the day making measurements at intervals.

Results: Figure 15 shows, for each eye of two subjects, the log/log plots of the measurements of the aftereffect (S cm) against time spent in the light since the end of McCollough exposure.

Findings: For the first 5 min after removal of the goggles, readings on the dark adapted eye were a bit erratic but subsequently the readings and subjective appearance of the hues seen on the test field became very closely similar for the two eyes.

The pair of runs (of VM, figure 15b, c) rule out the possibility that a steady bias in either eye was spuriously rendering the time coursesparallel.

Conclusion: The McCollough effect does not decay appreciably during 24 hours of darkness.

The fact that in figure 15 b and c the results for the 'covered' eye droop slightly below those for the eye exposed 24 hours later, may be attributable to random 'thermal' processes and suggests that over a period much longer than 24 hours storage might begin to fall.

5.4.2 Retention of the McCollough effect in darkness; other authors

Skowbo et al. (1974) have claimed that the McCollough effect decays by the same amount in the 'natural environment' and 'in darkness'. It must be pointed out, however, that their periods of 'darkness' included 12, 35 min of 'exposure to homogeneous fields in experiments II, I respectively'. The percentage of decay which they observed in these experiments accords well with that observed by Riggs et al. and ourselves after similar times (12 and 35 min) spent in the light. Diane Skowbo has since written (personal communication, 1974) that she has 'induced effects in both eyes and had subjects wear an eye patch (black) over one eye for several hours. After this period, the effect appeared stronger in the eye that had been occluded.'

5.4.3 Decay of the McCollough effect at scotopic and mesopic levels of illumination

Decay of the McCollough aftereffect appears to be brought about by having light enter the eye and to be arrested when light is cut off (5.3.1). The question arises as to how sharply and at what luminance level the changeover from decay to no decay occurs. Stromeyer (1974) has found that the McCollough effect is visible at very low scotopic levels of illumination (below 10^{-4} ml, see 2.4.7). Does it then decay at these luminance levels? Does an alteration of rate occur in the region of the rod/cone break in the dark adaptation curve?

The experiment below was in the nature of a pilot study on one subject, for although the qualitative findings are of a sufficiently interesting kind to justify more attention, the experiments ran up against a snag. This snag is that the state of adaptation of the eye is different at the end of each of the periods spent at a different steady luminance, and this probably affects the hue match settings appreciably for at least a minute or two (cf. 5.3.1.1).

Experiment 5.4.3.1 Decay of the McCollough effect at various luminance levels

Runs were performed in the manner of experiment 5.1; a McCollough exposure lasting 10-30 min being followed immediately by about 4 readings lasting for at most 3 min. The subject then spent up to 2 hours in normal laboratory surroundings at one of 6 steady luminance levels, ranging from the normal indoor level (40 cd/m^2) to near darkness (7 x 10^{-4} cd/m^2). At the end of this period the subject viewed the test card T_2 at 0.5 log ft L and made the hue match settings as rapidly as possible. Further readings were taken at intervals later, with life at ordinary levels of illumination intervening.

To attain the lower luminance levels the subject wore neutral density filters continuously for the two hours (and additional blue filters for the runs at scotopic levels). In some runs an artificial pupil was worn on one eye to test whether this made a noticeable difference to decay. Two stripe widths* (2.5 and 1.3 cycles/degree) were used on different occasions for some mesopic and scotopic runs. The wide grating was used so that the aftereffect could be visible on a test field with resolvable bars and be viewed for a considerable part of the two hours. The broad inducing patterns subtended 70° x 70° at the subject's eye.

To test the possibility that, at scotopic levels of illumination, decay might be greater in regions where the density of rods is high, a comparison was made after 2½ hours at 2 x 10^{-3} ml of readings performed a) viewing the 'windows' of the test field foveally and b) fixating (with the right eye) near the right hand apex of test field T_1 i.e. some 8° from the 'windows'.

Findings: The McCollough effect was visible, on suitable test cards, at all of the above luminances. In the mesopic range as Stromeyer (1974)

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* The test field T_2 with measuring apparatus M_1 was viewed from 65, 46 cm to approximately match these inducing stimuli.

reports, the colours are more saturated (when the test card is at about 0.3-1.5 cd/m^2) than at any other level. In the upper part of the scotopic range (above 5×10^{-3} cd/m^2) both green and pink McCollough hues were clearly visible. At lower levels (about 2×10^{-3} cd/m^2) only the difference in pinkness between the two halves of the (1.3 cycles/degree) test field was detectable and one had to wait for from 2-10 seconds for this colour to 'come up' by what felt like a process of integration. After a 20 min McCollough exposure the threshold for seeing the aftereffect was at 1.2×10^{-3} cd/m^2.

Table 8 shows that at scotopic levels no appreciable decay occurred. Even above the rod/cone break at 0.3 cd/m^2, decay was still zero. With increasing luminance decay gradually increased. At dim indoor levels

Table 8 Variation with luminance level of the decay, β, of the McCollough effect

Date	Luminance level	Duration (min)	$\beta\left(= \frac{\log \frac{S_1}{S_o}}{\log \frac{T_1}{T_o}}\right)$
5.11.76	43 cd/m^2	40	0.30
18.4.75	1.1 cd/m^2 (unpatterned white field)	20	0.12
30.11.76	0.3 cd/m^2 just above rod/cone break	129	near 0
25.10.76	1.7×10^{-3} cd/m^2	152	0
29.10.76			0.03-0

(10 cd/m^2- 27 cd/m^2) it was found that exposure to the achromatic test fields exerted a marked influence on the rate of decay even though the lighter areas of the test card had a lower luminance than the lighter

areas of the environment. Brief, occasional exposures to the gratings were sufficient to double the overall value of β during a period of two hours. At 43 cd/m^2 the effects of testing were much less marked (as remarked in 5.2.4.3).

In those runs at the lowest intensity levels in which no decay occurred during two hours of wearing filters, subsequent decay when the goggles were removed was rapid. If the time origin was taken at the time when normal illumination (about 40 cd/m^2) was readmitted to the eyes, β took values in the range -0.26 to -0.35.

Conclusions: Although the McCollough aftereffect is visible down to 1.2 x 10^{-3} cd/m^2 and particularly strongly visible in the mesopic range only moderate decay of the effect occurs in the ordinary environment at mesopic levels and probably none at scotopic.

At modest luminance levels,exposure to pattern is a more powerful factor than the ambient luminance level in bringing about decay.

5.5 Does the McCollough mechanism undergo no change in darkness?

The experiments above (5.4.1.1, 5.4.1.2), demonstrating retention of the McCollough effect in darkness, might at first seem to show that the state of the McCollough mechanism is completely 'frozen' whenever light is not entering the eye. On this view, however, it would be expected that when the decay of a McCollough aftereffect is traced from the day of induction through to a second day, the second day's readings could be brought into line with those of the first day simply by omitting, from the abscissa, the hours spent in darkness. It will be remembered that in experiment 5.1 the readings for the second day of the decay process did not fall upon the extrapolation of the first day's graph on any coordinates tried, and a slope was obtained some ten times steeper than that of the first day when plotted on log/log coordinates. Figure 16 shows the effect on such results of omitting (at the vertical dotted lines) the hours spent in darkness at night. It makes it clear that even when only the time spent in the light is counted, the results for later days still fall very steeply and are not brought into a simple relation to those for the first day. (The latter point is true on other co-ordinates too.) So although the McCollough effect undergoes decay only in the light, the state of the mechanism mediating the aftereffect is not frozen in darkness. The situation evokes rather the image of a 'cease-fire' during which forces are redeployed behind the lines, to better advantage, so that when hostilities resume they do so with greater vigour and effectiveness than before the interruption!

As the second day's points follow a curve somewhat similar to that of the first day (cf. figure 10c) it seemed possible that the time of waking on the second day was the new zero for a refreshed decay process. Table 9 summarises for several runs from experiment 5.1, the effects on

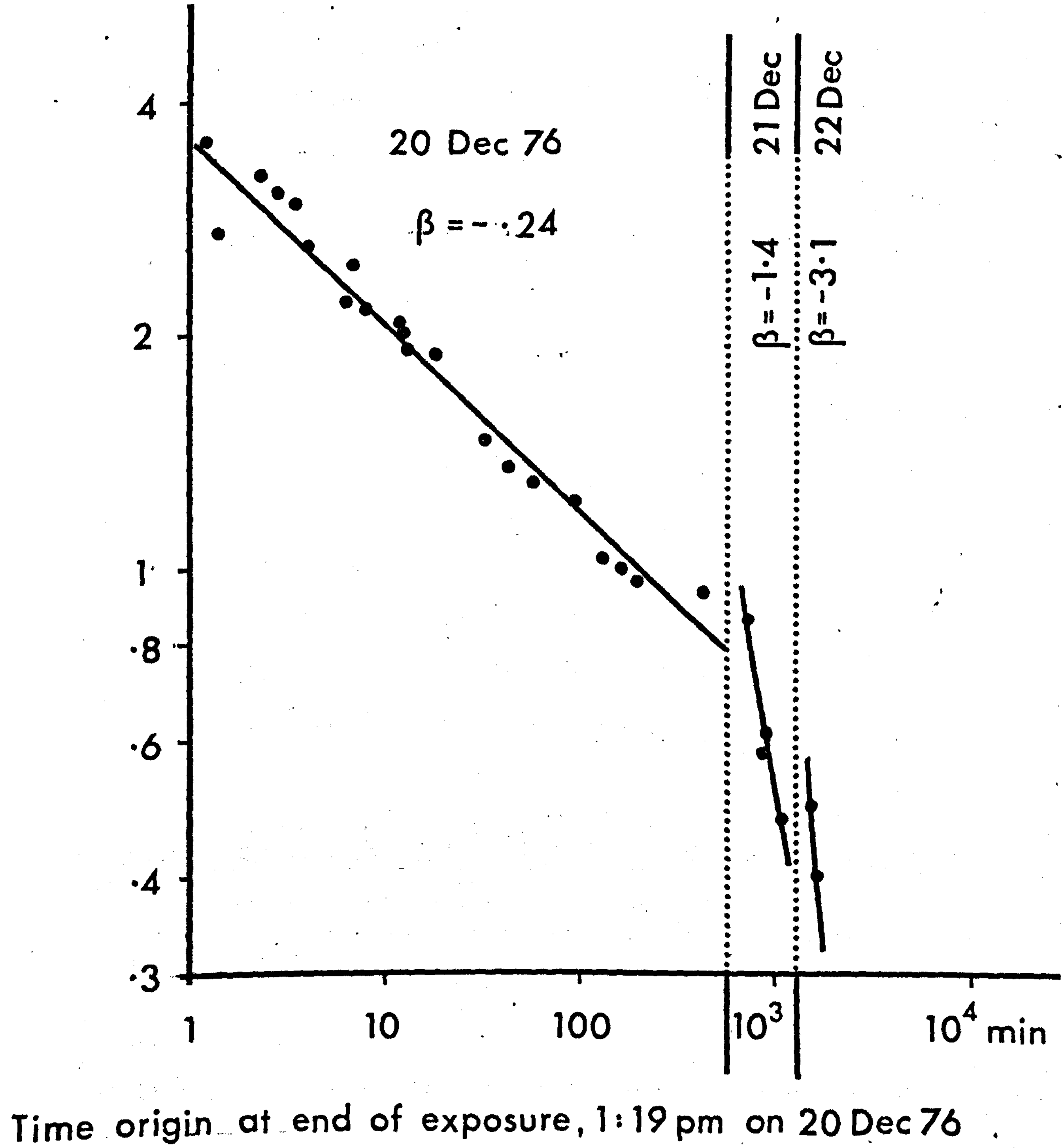


Figure 16

The decay of the McCollough effect as a function of time spent in the light since end of McCollough exposure (log/log plot). Dotted lines indicate where the hours of darkness at night are omitted.

the second day's log/log slope of computing the time in different ways. For columns a) and b) the time zero is at the end of the McCollough exposure; for a) the total time elapsed is plotted, for b) the 500 or so min of darkness at night are omitted. For c) the time zero is taken at the minute of waking on the second day. (Results were also calculated, in view of the ideas of Jones and Holding (see 5.6), with time zero at the taking of the first reading on the second day. But the points then no longer fell on straight lines and the slopes of the groups of points became very miscellaneous.)

The values of β given in table 9 are only approximate because the range of values through which the aftereffect fell on the second day was not large (typically S dropped by only 0.3 or 0.6 cm); the number of readings was not large (upwards of three) and readings did not commence until at least an hour after waking. Nevertheless it was noticeable that taking the time origin at or near the time of waking (column c) systematically gave the straightest lines, and for these β took values similar to, or only slightly steeper than, those for a newly induced effect. Figure 17 shows a typical plot. (In figure 28 c, experiment 6.3.1 , these same results are shown with the time zero at the end of the exposure: β is then -3.0.)

The second day's decay was more closely investigated by inducing an effect in the evening so that the range of values covered next day should be larger.

Subject VM

End of McCollough exposure		Overnight dark period	Time of waking on second day	Slope, β, of log/log plot		
Time	Date			a	b	c
9.50 am	5.2.73	540 min approx.	7.45 am approx.	-1.1	-0.72	-0.20
11.24 am	13.8.73 figure 9 (20 min)	540 min	7.45 am approx.	-2.30	-1.50	-0.53
12.50 pm	6.11.73	460 min approx.	7.40 am approx.	-3.60	-2.40	-0.50
12.17 pm	9.12.76 figure28c	480 min	8.00 am	R -1.20 L -2.60 Both -2.50	-0.82 -1.80 -1.70	-0.22 -0.47 -0.43
2.40 pm	17.3.77 figures 17,28d	540 min approx.	7.42 am	-3.00	-1.70	-0.41
R 11.04 am L 1.19 pm	20.12.76 fig 16	555 min approx.	7.45 am approx.	R -3.50 L - 2.80	-1.60 -1.40	-0.54 -0.50

Table 9 The slope, β, of the aftereffect's decay on the day following a McCollough exposure, time being computed as:

a. total time elapsed from end of McCollough exposure;
b. total time spent in the light since end of McCollough exposure (night time omitted);
c. time spent in the light since waking on the second day.

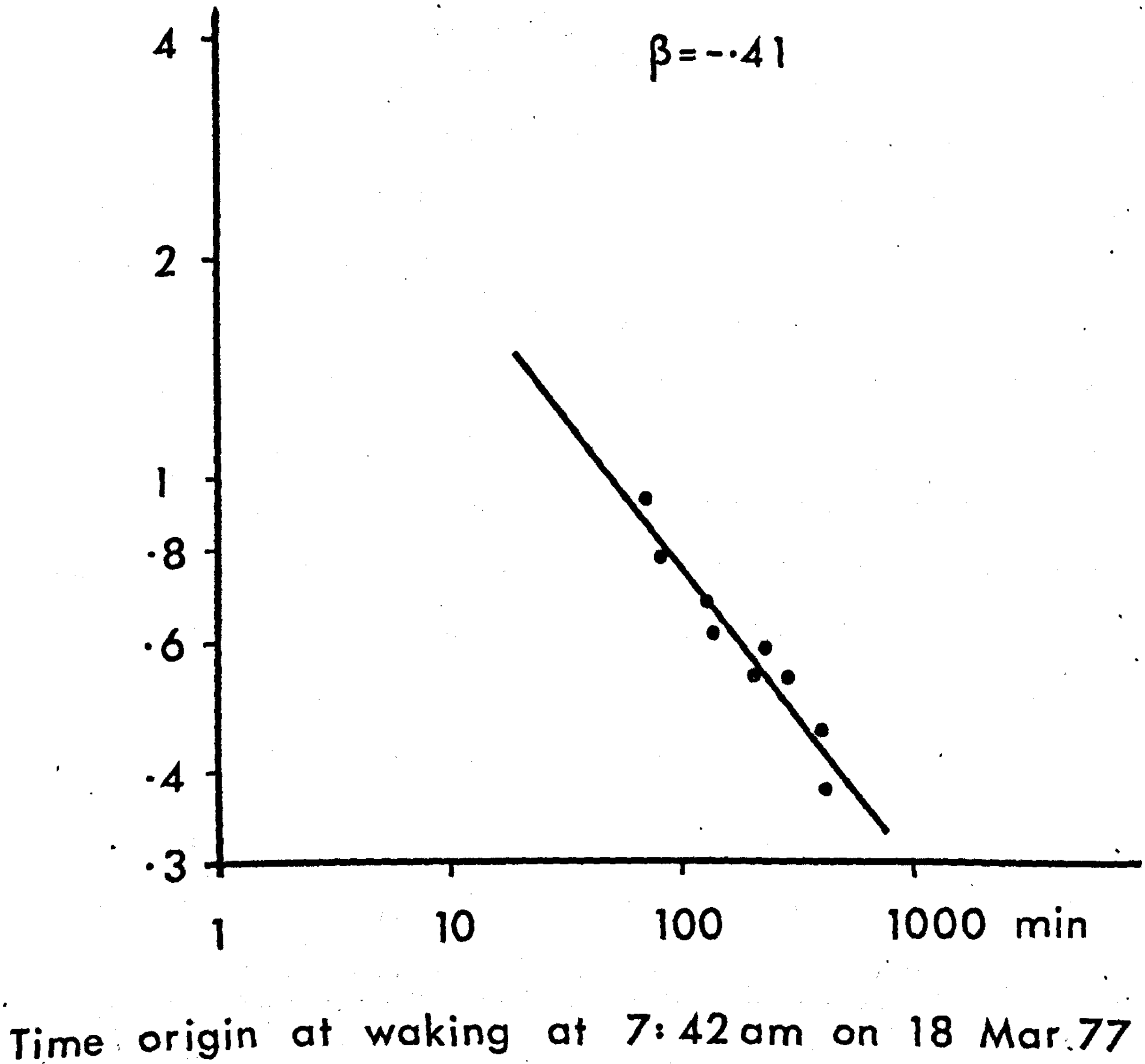


Figure 17

The decay of a McCollough effect during the day following the McCollough exposure, plotted on log/log coordinates with origin at the time of opening the eyes on the second day (18 March 1977).

Experiment 5.5.1 To investigate whether an aftereffect which has already decayed somewhat resumes where it was interrupted by darkness

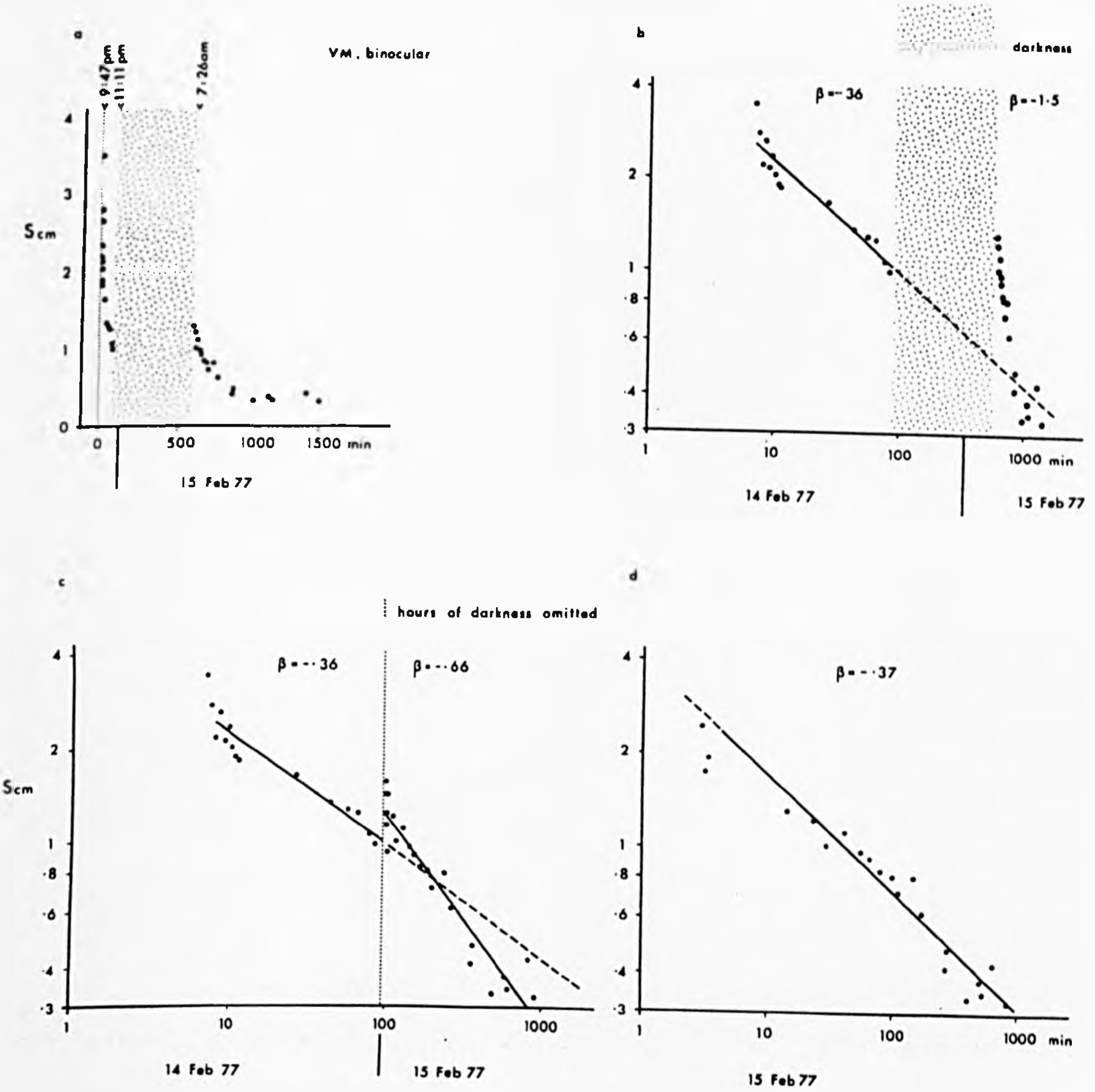
Apparatus M_1 with test card T_2 at 0.5 log ft L was viewed from 97 cm while making the pre and post exposure measurements binocularly. The inducing exposure was to alternate red and green oblique gratings viewed binocularly in a tachistoscope (E_5). A presentation cycle of 9 sec on, 9 sec off was used during a 20 min exposure.

At the end of the exposure the subject spent 0.8 min in the dark then 85 min continuously at 0.5 log ft L making readings and engaging in normal indoor life. The subject then put on light tight goggles and went to bed near the apparatus. After 496 min of darkness the apparatus and room lights were switched on again (0.5 log ft L) and the goggles removed at 7.27 am. Further hue match settings were made immediately and throughout the day (15 February 1977).

Results: Figure 18 shows the decay of the McCollough aftereffect, a) on linear/linear and b), c) and d) on log/log coordinates. In a), b) and c) the time origin is at admission of light to the eyes just after the end of the McCollough exposure; in d) it is at the opening of the eyes in the light on the second day.

Findings: The graphs show the features which have been remarked above, but here, as there is nearly one log unit of decay on the second day, the conclusions can be drawn with much greater confidence.

Rate at which decay resumes: The results for the second day's decay do not fall on the extrapolation of the first day's curve on any coordinates a) b) - even when the hours of darkness are omitted, c) When the second fig 18 Decay of McCollough effect on the day after induction



a,b,c: Time origin at 9:47 pm on 14 Feb 77
(end of McCollough exposure, 9:46 pm)

d: Time origin at waking, at 7:26 am on 15 Feb 77

day's readings are plotted on log/log coordinates with time origin at the moment of admitting light to the eyes on the second day, they fall on a straight line of about the slope usually found following exposure on the first day. A slope of -0.37 in d) is to be compared with $\beta = -0.36$ in the early part of b)

Level at which decay resumes: For 30-40 min after the opening of the eyes on the second day the aftereffect was judged to look subjectively as strong or stronger than it had before sleeping the previous evening, and the hue match settings independently confirmed this impression. (The subject considered that all uncomfortable and detectable signs of dark adaptation had passed off after 7 min.)

Conclusion: When a McCollough aftereffect which has already been decaying for some time is interrupted by a period of darkness, the aftereffect i) does not decay in darkness but, ii) does not resume its course at either the rate or the level at which it was interrupted by darkness. The rate of decay is more rapid than before the period of darkness, taking a form similar to that of a newly induced McCollough effect (with time origin at the time of admitting light* to the eyes). The magnitude of the aftereffect does not decrease and if anything recuperates.

5.5.2 Summary: The effects of light and of darkness on the decay of the McCollough effect

The rate of decay of the McCollough effect is influenced by the amount of light entering the eye. At ordinary light levels (1.0 log ft L upwards) and with continuous illumination, its decay course proceeds at what we might call the 'standard' rate; the magnitude of the aftereffect is halved for every 8-fold increase in the time spent in the light, time being measured from the admission of light to the eyes after the end of

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* In view of the findings of section 5.4.4.1 that very little or no decay occurs at dim luminance levels where the subject can nevertheless see tolerably well, the luminance level should probably be specified here as at least 0.5 log ft L.

the McCollough exposure. At low light levels (below 0.5 log ft L) the rate of decay is slower. In darkness no decay occurs.

When a period of decay in the light is followed by a period of darkness (e.g. a night's sleep) the subsequent decay does not resume where it was halted by darkness, but proceeds - as if freshly induced - at about the 'standard' rate.

The latter facts suggest that though it is the admission of light to the eye which promotes events which gradually lead to the resetting of the state of the visual mechanism, the use of the eye depletes a reservoir of some material or condition which can only be restored when light ceases to enter the eye.*

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* This idea suggests that the decay rate of the McCollough effect might be influenced by the length of time that the subject has been awake. A small 'time of day' effect has been found (5.3.6.2)

5.6 The time origin of the decay process

We have already given some consideration to the question as to what time should be taken as origin for the decay of the McCollough effect(4.3.3.1, 5.1.2.4, 5.3.2, 5.4). The time at which light is admitted to the eye after a period of darkness appeared to be the origin for the power law decay during the ensuing period in the light. The next experiment (5.6.1) brings out further evidence supporting this view.

In 1975 Jones and Holding made the interesting suggestion that, in the absence of testing, in the normal environment decay proceeds very slowly, and that it is the viewing of achromatic gratings which initiates the kind of decay process which has been hitherto reported - 'introducing a test seems to begin a decay process'. Once started by a first test this decay process continues in the absence of further testing. These claims were based on the following experiment. Subjects in groups of 10-16 were exposed for 15 min to McCollough stimuli. One group made measurements on their aftereffect immediately, the others when intervals of 8-120 hours had elapsed. Only at 56 hours and 120 hours (2 & 5 days) were there significant differences between the groups; at the fifth day, the average aftereffect for those subjects who were being tested for the first time was six times larger than for those who had already been tested one or more times.

They offer two possible interpretations of their data; in terms of an 'extinction trial' and of the 'rendering of the memory trace labile by recall'.

Experiment 5.6.1 investigates Holding and Jones's claim that 'simple decay seems to have little or no effect over the intervals (8-120 hours) tested'.

Experiment 5.6.1 Decay of the McCollough effect in the absence of testing

Using the methods and apparatus described in experiment 5.1, four experiments were performed on one subject in which the first test was not made until the subject had spent 24 hours, 4 hours, 10 min, 4 min in ordinary light. For the first two experiments this period was spent in ordinary life, in the other two it was spent viewing a large plain white card at 1.1 log ft L. For each run there was an appropriate control run at another time either in the same eye or the other eye.

5.6.1.1 Delayed test at 24 hours

The McCollough exposure was binocularly for 20 min to a red vertical and green horizontal grating (2.2 cycles/degree) using a presentation cycle of 7 sec on, 1 sec off. The right eye served as control. Its aftereffect reading was 4 cm immediately after exposure. After twenty-four hours spent in ordinary life both eyes registered 1 cm and the aftereffect was judged marginally stronger with the left eye.

5.6.1.2 Delayed test at 4 hours

Four identical binocular exposures to oblique red and green gratings (1.3 cycles/degree) were performed within a two month period. Three were controls in which the aftereffects in each eye were measured immediately after exposure. Figure 19a shows (unfilled symbols) the results for one of these controls, and (filled symbols) the aftereffects in the two eyes on the 'delayed test' run.

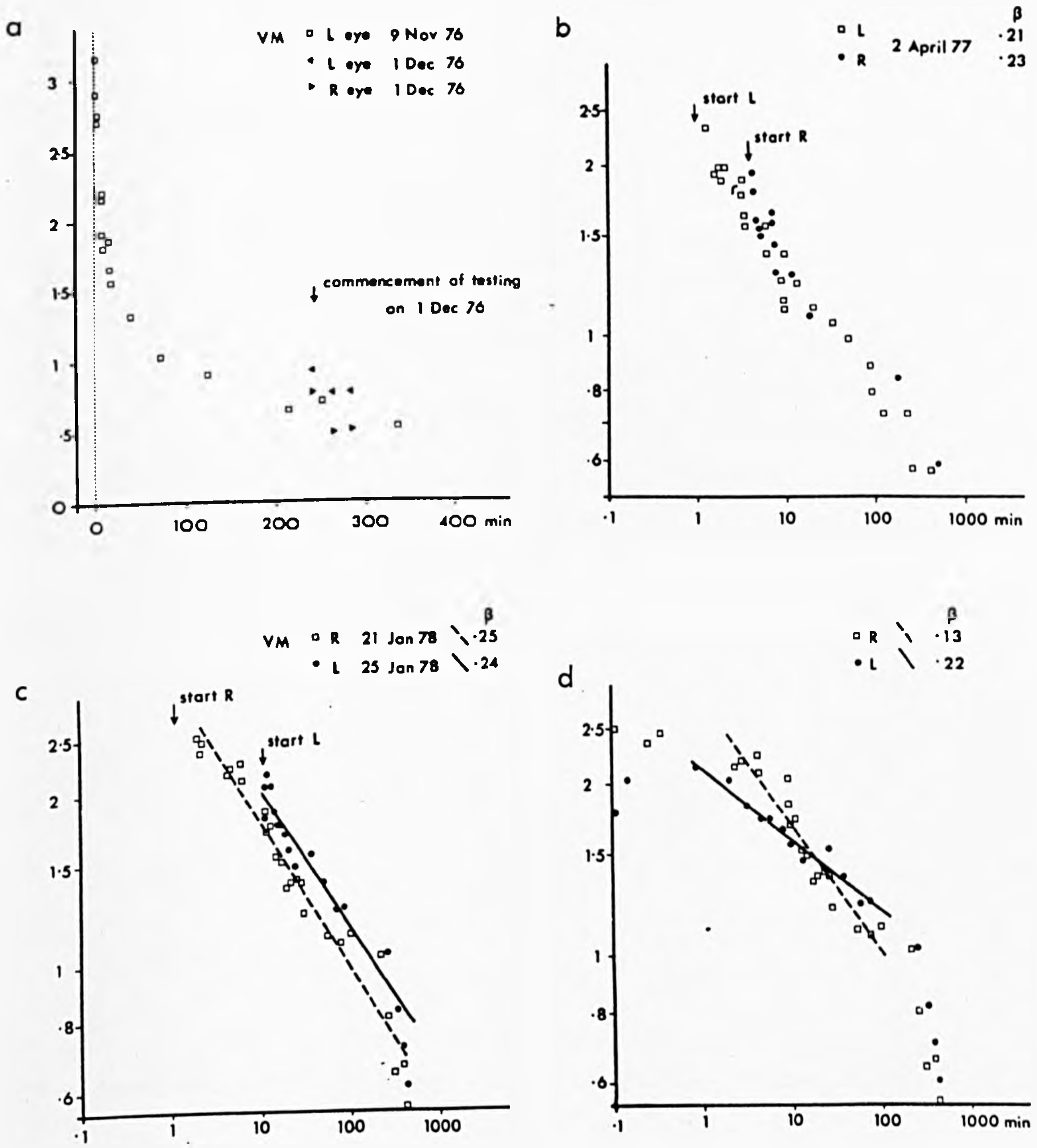


Figure 19 'Delayed testing' vs. testing shortly after the end of the McCollough exposure

The magnitude and subsequent decay of the McCollough effect when the first test is not made until (filled symbols) a) 4 hours, b) 4 min, c),d) 10 min after the end of the McCollough exposure. In control runs (open symbols) testing commenced 1 min after the end of the exposure. Figures a), b), c) have time origin at the admission of light to the eye shortly after the end of the McCollough exposure. In figure d) the data of figure c) are plotted with time origin at the commencement of testing (arrowed in c)).

5.6.1.3 <u>Delayed test at 4 min</u>

Identical 8 min monocular McCollough exposures to gratings of 3.2 cycles/degree were given to left and right eyes respectively at 9.56 am and 1.56 pm on the same day. Following exposure, 0.8 min was spent in darkness, and then 1 min, 4 min respectively in gazing, with defocussed eyes, at a white card subtending 60^{o} and illuminated at 1.1 log ft L. Figure 19b shows the subsequent monocular measurements of the aftereffects made at a steady luminance of 0.45 log ft L (10 cd/m^2). These log/log plots have time origin at the moment when light was admitted to the eye. Arrows mark the start of viewing the test gratings for each eye.

5.6.1.4 <u>Delayed test at 10 min</u>

The right and left eyes were given identical 10 min McCollough exposures at 10.30 am on different days. The white card was viewed, as above, for 1 min, 10 min respectively on the two occasions before readings commenced. Figure 19c shows the measurements on log/log coordinates with time origin at the admission of light to the eye. Figure 19d shows these results replotted with time origin at the arrows, i.e. at the commencement of viewing the test field.

<u>Findings</u>: Throughout their decay courses the magnitudes of the results for the delayed test run and the control run are closely similar at equal times after the admission of light to the eye. They are <u>not</u> similar when compared at equal times after the first test. There are signs that the first reading in the delayed test cases is marginally above the control, and drops rapidly during the first minute of testing, but this may be no different from the pattern of rapid decay already observed within most groups of readings during the exposure to gratings (5.3.3.1 and 5.3.4.1).

5.6.1.5 Conclusion:

Provided that light at normal intensities (above 10 cd/m^2) is entering the eye the general form of the decay course is closely similar whether a test has been performed or not. Even unpatterned light produces decay. There seems no reason to think, with Jones and Holding, that only a small decay of the McCollough effect takes place in normal light in the absence of testing, nor that exposure to a test grating is a necessary 'trigger' for a more rapid decay process.

5.6.1.6 Discussion

Since all the above experiments used monocular measurement they leave open the possibility that the binocular component of the McCollough effect (6.3.1) may behave differently. Runs similar to those above, but using binocular exposure and testing have, however, been performed by Keith White (1976, p. 27) who found (with delayed tests at 1 hour to 7 days after exposure) 'no large or systematic differences which could be attributed to the repeated vs delayed test sequences'.

How then can we account for the results of Jones and Holding? Keith White points out, being familiar with the apparatus used by Jones and Holding, that the readings upon which Jones and Holding base their comparisons all correspond to very small saturations. He mentions that the largest difference between groups after 24 hours is smaller (by 36%) than the difference which Fidell had obtained between subjects, none of whom had been exposed to a McCollough stimulus!

The real puzzle therefore is how Holding and Jones obtained such small readings from the group who were tested at 0 hours. Inter-subject differences cannot be ruled out as a contributory factor (cf. 5.1.2, 5.8.1) but a second possibility is that the use of a cancellation technique without any comparison area (2.8.4.5) led to spuriously low readings for the stronger aftereffects.

5.7 The additivity of McCollough aftereffects induced at different times

The rate at which the McCollough effect decays depends not only upon its current strength but also upon the length of time for which it has been decaying. Thus two aftereffects of equal size may have decay rates $(\frac{dS}{dt})$ differing by a factor of 100, if one is the aftereffect of a recent short exposure and the other the result of a long exposure which ended several hours previously. The question naturally arises as to what happens when two exposures are administered to one eye with an interval of minutes or hours between them. Does the second exposure obliterate the aftereffects of the first or can both aftereffects proceed simultaneously in one eye? If so, do they proceed independently or is there interaction?

Experiment 5.7.1 A qualitative demonstration of residual aftereffects

The apparatus and methods of measurement were as in experiment 5.1. The inducing stimuli were red and green oblique gratings (2.5 cycles/ degree) presented by the two projectors (E_1) to the left eye. Apparatus M_1 with test card T_2 at 96 cm was used for measuring the aftereffects.

Over a period of 10 days the subject was exposed to McCollough stimuli for periods of 8-20 min almost every day. (See diary below figure 20.) From 21-25 May the stimuli had one pairing of colour and orientation and on the final two days, 26, 27 May, the pairing was reversed.

Figure 20 shows a linear/linear plot of the aftereffect measurements from 22-28 May.

Findings: From 22-25 May a progressively larger bias was accumulated from day to day. On the 26 and 27 May the aftereffect decayed, after the reverse exposure, with abnormal rapidity (β = -0.67, -0.53

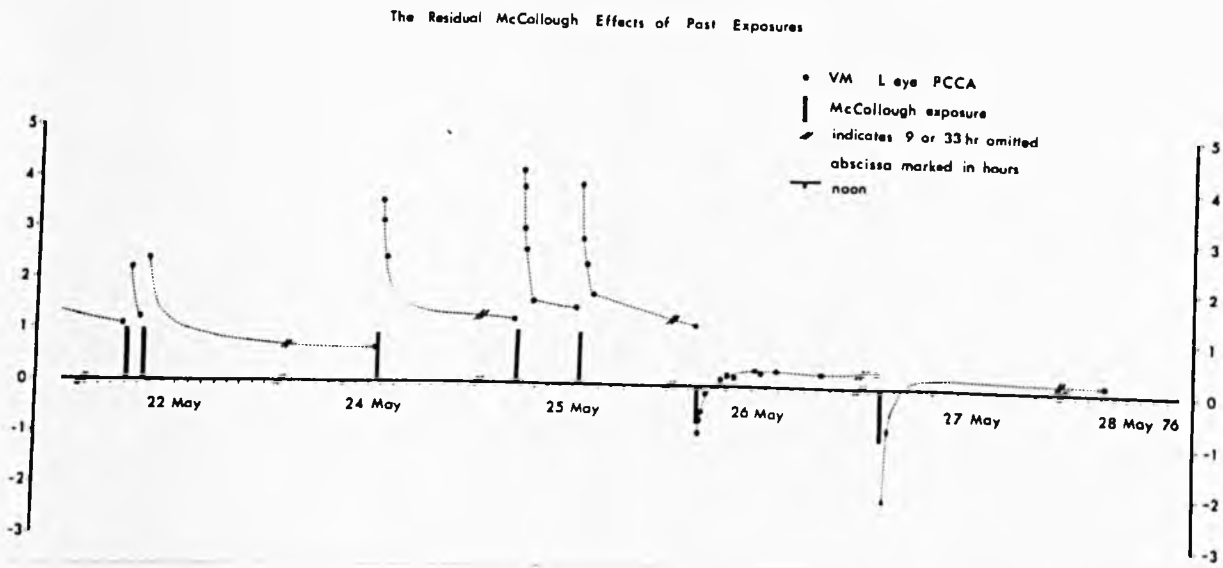


Figure 20

Diary of McCollough exposures, May 1976

	Red	Green	Green	Red
18 May	20 min	8.53-9.13 pm	10 min	9.25-9.35 pm
19 May	20 min	9.28-9.48 am	8 min	10.35-10.43 pm
	20 min	11.10-11.30 am	20 min	5.00-5.20 pm
20 May				
21 May	20 min	4.01-4.21 pm		
22 May	20 min	10.01-10.21 am		
	20 min	11.26-11.46 am		
23 May	18 min	1.39-1.57 pm		
25 May	20 min	10.25-10.45 am		
	20 min	3.13-3.33 pm		
26 May			14 min	9.41-9.55 am
27 May			20 min	8.45-9.05 am
28 May				

←graph begins here (22 May)

←graph ends here (28 May)

respectively), passed through zero and reverted to the polarity of the preexposure bias. The observed aftereffect on both these days indubitably returned to the hues indicated by the measurements.

By June 1, with no intervening exposures to oblique McCollough stimuli the eye had returned to neutral and was showing, if anything, a very small reverse bias. The bias of the 26, 27 May is not therefore attributable to a permanent astigmatic bias.

In computing the values of β for the drop in aftereffect on the 26 and 27 May the magnitude of S was measured from the usual zero (corresponding to zero McCollough effect). But if we allow for the initial bias, taking it as a base level with a near steady value-in the region of 0.8-0.3 on each of the two days-which can be simply added to the readings, shallower, straighter log/log plots are obtained. Table 10 shows the variation of β, the slope of these plots, with the assumed value of the steady bias. Time origin is taken at the end of the appropriate exposure on 26, 27 May.

Table 10 The variation of β, the slope of the log/log decay, when a steady bias is added to the readings

Value of steady bias added to ordinate (cm)	β 26 May	β 27 May
0	-0.67	-0.53
0.3	-0.36	-0.32
0.4	-0.31	
0.5	-0.28	
0.6	-0.25	
0.7	-0.23	
0.8	-0.21	

It can be seen that when a steady base level is taken at about the level (0.7, 0.3) of the pre-exposure biasses for the respective days (26, 27 May) 'normal' values for the decay of the superimposed recent aftereffect are obtained in the region -0.2 to -0.3.

Conclusion: These results suggest that McCollough aftereffects are not completely obliterated by subsequent McCollough exposures, and that, at least approximately, the aftereffects from earlier and later McCollough exposures are straightforwardly added.

Discussion: Other authors

Other observers have independently remarked on the above swing back through (or from) zero. Keith Bradshaw (personal communication, 1975), performing experiments on the same subjects on successive days, routinely 'neutralised' the previous day's bias by giving a short McCollough exposure to the reversed stimuli. He remarked that in three-quarters of cases, though the aftereffect was reduced carefully to zero, it weakly reappeared after half an hour or more. Sigel and Nachmias (1975, footnote 4) have observed the same phenomenon.

In the above calculations (Table10) the earlier aftereffect was crudely assumed not to be decaying at all. Cases where both aftereffects are decaying appreciably will next be considered so as to see whether their two decay rates are separately preserved.

Experiment 5.7.2 To investigate the change in aftereffect strength and the form of the subsequent decay when a long McCollough exposure is followed at a later time by a second exposure.

Exposure and measurements were performed with the apparatus and general methods employed in experiment 5.1. The measurements were made using apparatus M_1 with test card T_2 viewed at 67 cm and 0.5 log ft L. Exposure was to red and green orthogonal oblique gratings (of 2.2 cycles/

Table 11 Magnitudes of a-e immediately before and after a McCollough exposure

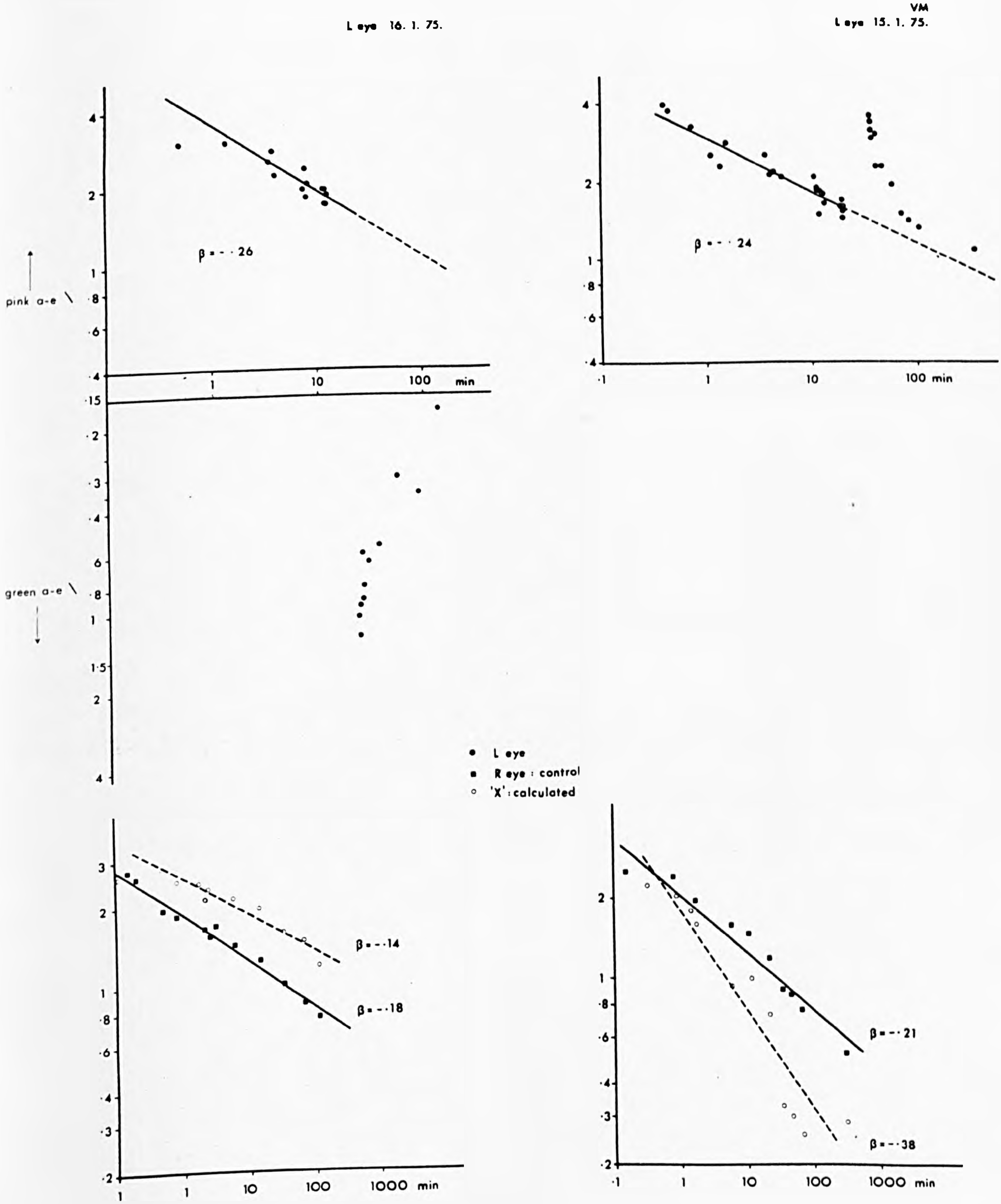
	Date		Second exposure condition & duration	Colour-orientation. Pairing of later exposure: Opposite to that of earlier exposure			Same as that of earlier exposure		
				A-e before	After	Magnitude of change in a-e	A-e before	After	Magnitude of change in a-e
Long second exposure	16 Jan. 1975	L	Binocular	-1.90	-1.05	+2.95			
	figure 22b		Same						
		R	9 min				+0.24	+2.60	+2.36
	15 Jan. 1975	L	Binocular				+1.50	+3.60	+2.10
	figure 22a		Same						
		R	14 min	-0.23	+2.50	+2,73			
Short second exposure	20 Jan. 1976	L	Binocular	+0.74	-0.07	-0.81			
	figure 23a		Opposite						
	figure 23b	R	1.6 min				+1.21	+1.68	+0.47
Short (control): exposure	10 March 1977	L	Binocular	-0.14	+0.70	+0.84			
	figure 23c		Opposite						
	figure 23d	R	1.6 min	+0.37	-0.59	-0.96			

Figure 21

Long second exposure

Colour/orientation pairing reverse of that of first exposure.

Colour/orientation pairing same as that of first exposure.



degree) presented by the two projectors (E_1) and viewed at 96 cm. A presentation cycle of 6 sec on, 3 sec off was used throughout.

One eye was given two McCollough exposures separated by an interval of over 20 min, the strength of the aftereffect being measured at frequent intervals before and after the exposures.

In separate runs the pairing of colour and orientation during the second McCollough exposure was the same or the reverse of that used for the first exposure. The second exposure was either 'short' (1.6 min) or 'long' (9 or 14 min) as compared with the first (20 min).

The other eye was also exposed as a control during either the first or the second McCollough exposure, being covered by a black patch during the remaining exposure. The aftereffect in it was also measured at intervals. Between making measurements and viewing stimuli the subject engaged in normal indoor life (at about 14 ml). On several other occasions, when the eyes were as free of bias as possible, 'short' monocular McCollough exposures (of 1.6 min) were given and the aftereffects measured under conditions which replicated those which had obtained above.

Results: Table II shows the magnitudes of the changes in aftereffect strength produced by the 'long' and by the 'short' exposures. Figures 21 and 22 show results corresponding to the 'long' and 'short' second

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* Figure 21

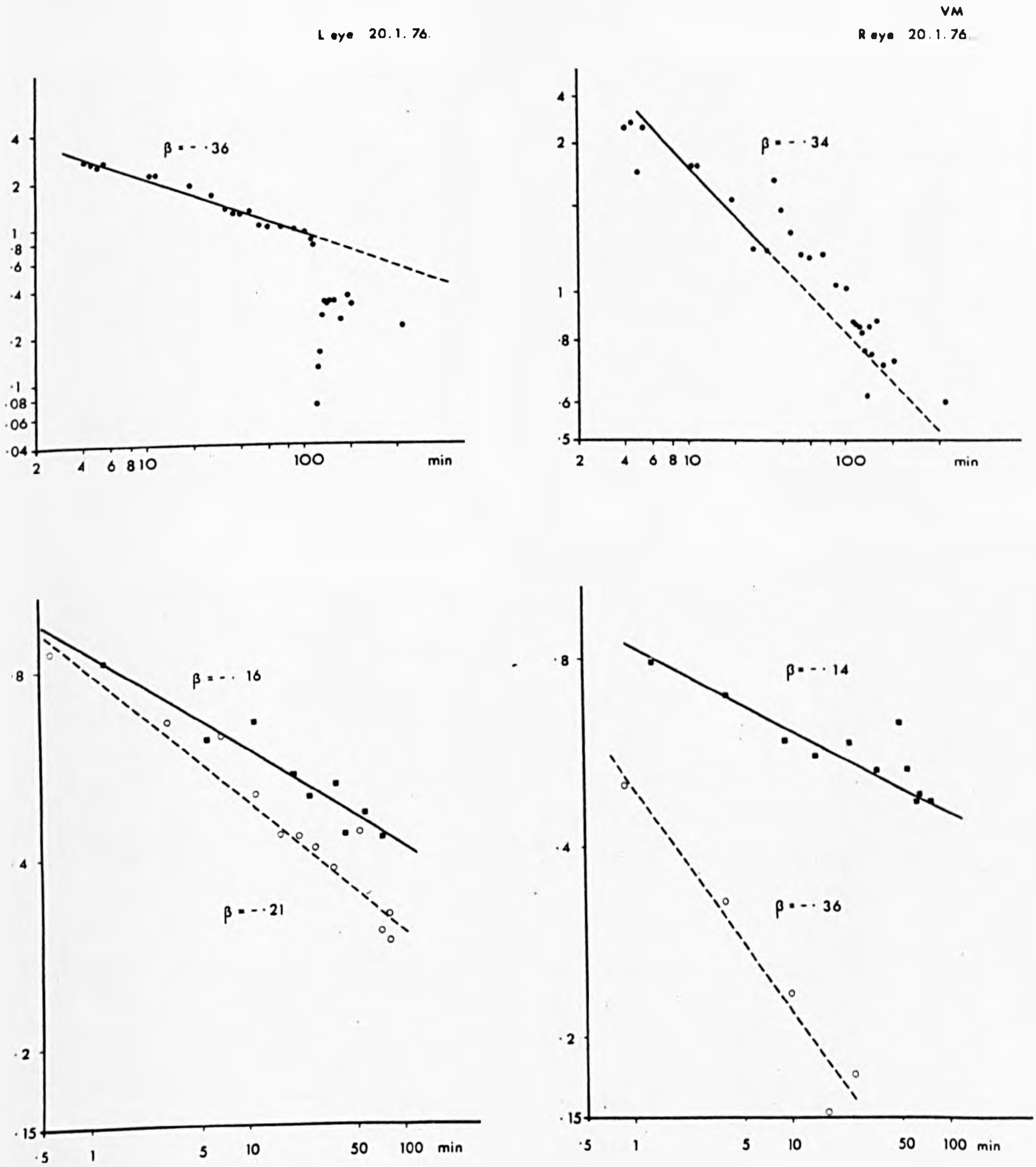
The resulting decay course when two exposures are given on one day to the same eye. A monocular exposure to the left eye was followed after an interval of 13, 23 min respectively by a long binocular exposure to stimuli whose pairing of colour and orientation was a. the reverse and b. the same as those of the first exposure. The durations of the first and second exposures were respectively a. 20, 9 min, b. 20, 14 min (log/log plots with time origin at end of first exposure) of 'X', the difference calculated from a., b. respectively, between the readings following the end of the second exposure and the level of the extrapolated decay course of the first aftereffect (dotted). (Log/log plots with time origin at end of second exposure.) Filled symbols show the decay of the effect in the control eye.

Figure 22

Short second exposure

Colour/orientation pairing reverse of that of first exposure.

Colour/orientation pairing same as that of first exposure.



exposures. The decay of the aftereffects in the eyes which received two exposures are shown in parts a) and b) of figures 21 and 22 on logarithmic coordinates with the end of the first exposure as time origin. (Negative values of S corresponding to a reversal of hue, present a difficulty on the logarithmic scale and have been plotted downwards from the second axis in figure 21a. Parts a, b show the results for runs in which the two successive exposures had, respectively, the same and reversed pairings of colour and orientation. Parts c, d of each figure show (open symbols) 'X', the difference (calculated from a, b respectively) between the readings which follow the second exposure and the extrapolated decay course (dotted) of the first aftereffect. For these log/log plots the origin is at the end of the second exposure. For comparison, the aftereffects produced in a previously unbiassed eye by an exposure identical to the second exposure are also shown in c and d (filled symbols).

Findings: Table II shows that the change in aftereffect strength as a result of a second exposure is in general slightly smaller when the first and second exposures have the same pairing of colour and orientation, than when they have reversed pairings. The difference is in keeping with the gradual approach to saturation during a continuous exposure to

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Figure 22

The resulting decay course when two exposures are given on one day to the same eye.

A thirty minute binocular exposure was followed after an interval of 39, 116 min respectively by a short (1.6 min) monocular exposure of the left and right eyes to stimuli whose pairing of colour and orientation was a. the reverse, b. the same as those of the first exposure. (Log/log plots with time origin at the end of the first exposure.) Figures c and d show (open symbols) the decay of 'X', the difference calculated from a and b respectively, between the readings following the end of the second exposure and the level of the extrapolated (dotted) decay course of the first aftereffect. (Log/log plots with time origin at end of second exposure.) Filled symbols show, for comparison, the effects produced on another day by identical 1.6 min exposures.

McCollough stimuli (see experiment 5.8.1)

Parts a), b) of figures 21 and 22 show the very rapid decay which follows the second exposure. When, however, it is assumed (figures c, d) that this decay consists of two independent parts - based on time zeros separated, as appropriate, by 13 or 116 min, the calculated decay of the later constituent takes the familiar power law form with β in the range 0.14-0.38. For those runs in which the pairing of colour and orientation in the second exposure was the reverse of that in the first, the decay rates, β, of the decay of X are particularly similar to those of the early part of a and the control in c. When the second exposure had the same pairing of colour and orientation as the first the decay of X was significantly steeper though it fell still within the normal range of values.

Conclusion: To a first approximation, the effects induced by an earlier and a later McCollough exposure decay independently. Each takes a power law course with its own time zero at the end of its own McCollough exposure. In the case of two successive exposures in which the pairing of colour and orientation is opposite, this independence of the two decay processes seems to be complete. When the stimuli are the same for the two exposures there are signs of some degree of interaction; the magnitude of the second aftereffect is slightly smaller and the decay rate a little more rapid than for the controls.*

* Keith White's (1975) similar independent study leads to the same conclusions as to differences in magnitude and decay rate.

5.7.3 'Neutralisation'

The above conclusions have a practical consequence for the conduct of experiments on the McCollough effect. Once a McCollough aftereffect has been induced the only way to remove it seems to be to wait for several days in the light. 'Neutralisation' by a further exposure to coloured gratings, only conceals (temporarily) the earlier aftereffect, by adding an opposite fresh aftereffect, and does not remove the original physiological bias.

5.7.4 The permanence of the record stored by the McCollough mechanism

If successively induced McCollough aftereffects lie, like archaeological layers, each pursuing its largely independent course of decomposition, this is a clue towards a picture of the mechanism of the McCollough effect. If changes, either in the cells themselves, or in the lateral connections between neighbouring cells, are envisaged as responsible for the McCollough aftereffect, these cells or connections must now be each imagined as undergoing 'recovery' or modification at a rate which depends upon how long ago their own modification was brought about and largely oblivious of later McCollough stimuli which, meanwhile, effect changes in other cells or intercell connections. The populations or sites corresponding to red and green at the same orientation are apparently completely independent, but there is a small degree of saturation and interaction at sites corresponding to the same colour and orientation.

5.8 Growth of the McCollough effect

It was intriguing that subjects in experiment 5.1 (e.g. figure 5) took widely different times to attain the same strength of McCollough aftereffect, and yet thereafter showed closely similar decay rates.

Hajos (1968) had found that the McCollough aftereffect strength increased with exposure durations (up to 16 min) in a fashion which yielded a nearly straight line on a log/log plot (of slope 0.31 to 0.44). The purpose of experiment 5.8.1 was to see whether the slope, or the intercept, or some other aspect of the growth curve, distinguished subjects who showed different rates of acquisition of McCollough after-effects.

Experiment 5.8.1 The McCollough aftereffect as a function of exposure duration

Apparatus: As in experiment 5.1 measurements were made using apparatus M_1 with test card T_2 at 65 cm from the eyes and exposure was to red and green oblique orthogonal gratings of 2.2 cycles/degree projected in a 6 sec on, 3 sec off cycle by apparatus E_1 onto a screen at 97 cm from the eyes. Chin rests were used for both exposure and testing.

The thirteen subjects were Ishihara normal and could read print 2 mm high and smaller at the distance, 97 cm, of the projection screen. All but VM were naive. Many of the subjects for this experiment were specially selected on the basis of a personality test (Edwards Personal Preference Schedule) as having extreme values of E (extroversion) and for N (neuroticism). * The testing of their McCollough sensitivity formed part of a more extensive exploration of their performance of various

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* Terms invented by Eysenck (1957).

visual and motor tasks by an undergraduate, Mr. M. Einarsson. Subjects were given practice in the hue matching task before they made their monocular pre-exposure settings.

The binocular McCollough exposure was interrupted after logarithmically increased intervals (typically 1.5, 3, 6, 12, 24, 36 min), for the rapid taking of 4 pairs of match settings on each eye. Each interruption of the McCollough exposure lasted about 2 min. The subject was asked to close his eyes while his chair was turned from the one chin rest to the other. Exposures were terminated when the subject's aftereffect brought him near the limit of the range of hue saturations which the apparatus could provide. Comments on what the subjects saw were not invited but the subjects generally made surprised remarks on the aftereffects. Those whose measurements seemed to point to larger effects commented on the colours after fewer minutes of exposure. The pink aftereffect generally evoked comment rather than the green but one subject (BP) remarked only on the green until, at last, after 40 min of exposure, he hesitatingly reported 'greyish pink' on the other half field (hitherto described as 'less green'). Figure 23 a shows results for two subjects whose build up rates fell at the extremes of the range and figures 23b and figure 30 (7.1.1.1) show results for a further three subjects. On the time axis is plotted the cumulative total time, T, for which the subjects had been exposed to the McCollough stimuli (i.e. omitting the time (about 5 x 2 min) spent in measurement). Table 12 summarises log/log plots for all thirteen subjects. It gives the slope, $\alpha = \dfrac{\log S_2/S_1}{\log T_2/T_1}$, and the level reached by their graphs after 20 min of exposure.

Fig 23

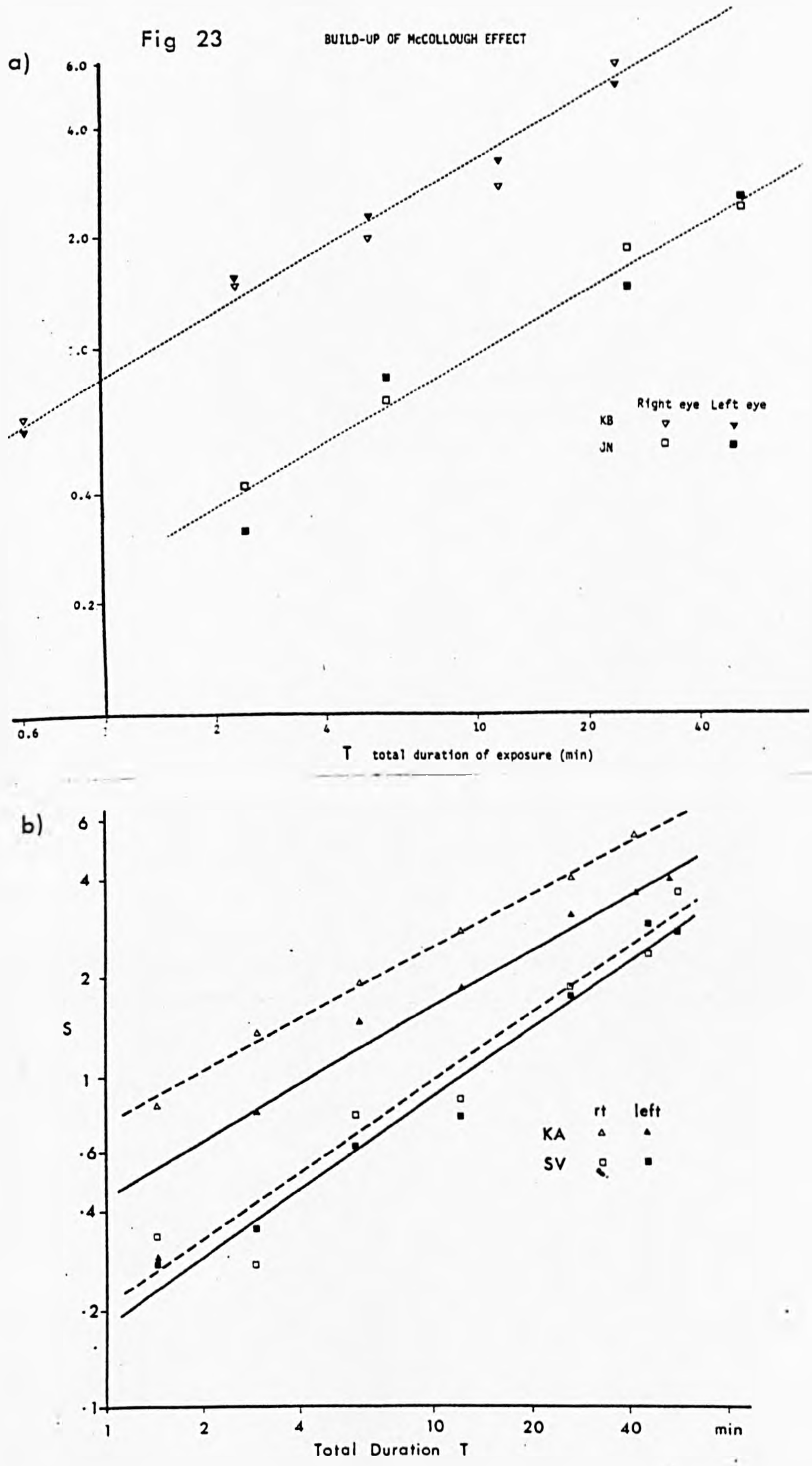

BUILD-UP OF McCOLLOUGH EFFECT
a)
6.0
4.0
2.0
0.4
0.2
0.6
2
4
10
20
40
T total duration of exposure (min)
Right eye Left eye
KB
JN
b)
6
4
2
S
1
·6
·4
·2
·1
1
2
4
10
20
40
min
Total Duration T
rt left
KA
SV

Table 12 Growth of the McCollough after effect as a function of Exposure Duration.

Subject		LA	KA	MA	KB	JI	SK	SM	VM	JN	BP	CR	LS	SV
Slope, α, of log/log plot	L	.63	.57	.74	.59	.72	.51	.69	.66	.58	.64	.66	.65	.67
	R	.63	.54	.60	.59	.82	.59	.69	.66	.58	.76	.65	.57	.67
Strength of McCollough Effect after 20min exposure	L	1.6	2.5	2.5	4.6	5.9	2.0	1.9	4.0	1.4	2.6	2.2	1.7	1.3
	R	1.7	3.6	2.3	4.9	6.2	1.8	1.9	3.7	1.7	2.2	2.4	1.4	1.4
Sex		F	M	M	M	F	M	F	F	F	M	F	F	M
Age		21	22	24	26	22	44	22	39	22	22	21	21	24

Findings: In every case the log/log plot of McCollough aftereffect strength against total exposure duration was a straight line.

The slope, α, did not differ greatly from subject to subject, or between the two eyes of any subject. The overall average value for α is $+0.64 \pm 0.07$. On the other hand, the aftereffect strength which subjects had acquired after any given time differed by as much as a factor of four and even the two eyes of one subject could show a considerable difference.

5.8.1.1 Source of intersubject differences

The origin of these large differences has not yet been identified.

The difference between KA's results for his two eyes suggested an optical origin for the differences. But KA's right eye had only marginally better acuity than his left . In other subjects too there was no obvious correlation of acuity with McCollough effect; thus, for example, SV's left eye had much better vision than his right and MA's right eye was distinctly better than his left.

Sensitivity to pale colours was measured in several subjects with the thought that it might be related to the separation of the spectral peaks for the subjects' red and green cone populations. The results for JI and JN (whose McCollough effect strengths fell at opposite extremes of the range) showed only a 20% difference in the saturations which they found just detectably pink or green (JN was the less sensitive).

Figure 23 Build up of McCollough effect

The growth of the difference S between hue match settings at the two oblique orientations for four subjects, plotted on log/log coordinates as a function of the cumulative total time spent exposed to the McCollough stimuli. In each case the two eyes viewed the same stimuli binocularly. Left eyes filled symbols; right eyes open sumbols.

Age of the subject does not appear to be a decisive factor: the four subjects of figure 23 were all aged 22-26 years.

Mr. Einarsson's study revealed no correlation of the differences in responsiveness to McCollough stimuli with E, N or any other parameters which he measured.

<u>Conclusion</u>: As a function of exposure duration, measurements of the growth of the McCollough effect fall on a straight line on a log/log plot, with a slope of $\alpha = +0.64$.

Although the growth rates, α, were so similar for all subjects tested, the intercepts of the plots differed greatly, and could also be widely different for the two eyes of one subject. The origin of these differences has not been identified.

5.8.2 Discussion: Other authors

These results give a higher rate of growth, α, for the McCollough aftereffect than those of Hajos, but accord well with those of Riggs (1974). I have already suggested (2.2) that the nett rate of increase in Hajos's experiment is slower than in that of Riggs et al. because considerable decay occurred during each of Hajos's lengthy and brightly lit interruptions for measurement. The similarity of our results to those of Riggs et al. suggests that our interruptions were sufficiently brief and dim to make no appreciable difference to the nett rate of increase.

5.8.3 The mechanisms of growth and decay

It is tempting to see a connection between the processes of growth and of decay of the McCollough effect.

Earlier in this chapter evidence has increasingly accumulated that decay of the McCollough aftereffect is not primarily an endogenous process, but a result of ongoing activity which takes place when light is entering the eye. If so, then both the processes of decay and of acquisition of the McCollough effect may be seen as instances of a single kind of modification of the visual system in response to the patterns of incoming events.

Since decay proceeds more slowly at lower light levels I have made a small investigation to check how the rate of growth of the McCollough effect depends on the luminance of the inducing stimuli.

The subject wore 3 mm artificial pupils and viewed the McCollough stimuli through neutral density filters covering (on different occasions) a 2 log unit range. The McCollough effects, acquired after 20 min exposures, increased linearly with the log of the stimulus intensity.* Further experiments are planned to determine whether it is the slope, α of the log/log growth graph or its intercept which is altered by the luminance change.

* Keith White (1975) obtained results on two subjects (without artificial pupils) which fall to either side of mine.

Chapter 6 Relations between the two eyes in the McCollough effect

Having two eyes makes possible a number of experiments for elucidating the locus of the McCollough type of effect. Below, these are termed dichoptic, transfer and binocular studies, though obviously these situations shade into one another.

The transfer section reports experiments in which only one eye was exposed to the McCollough stimulus. The dichoptic section deals with exposures of the two eyes synchronously to different stimuli, each eye's stimulus containing at least one aspect (colour or orientation) of the McCollough stimulus. Whereas in these two sections measurements were made monocularly, the binocular studies deal with measurements made using the two eyes to view the test card.

6.1 Dichoptic Studies

In November 1972 my husband and I found, as mentioned already in section 3.3.1 , that dichoptic presentation of the colour and pattern aspects of the McCollough stimuli produced orientation-contingent aftereffects in each eye (MacKay and MacKay, 1973). At just the same time Over, Long and Lovegrove (1973) were independently reporting negative results in 6 subjects following somewhat similar dichoptic stimulation (their 'dichoptic constant' condition). This led us to repeat and extend our investigations using improved versions of our presentation and measuring equipment. These experiments only strengthened our conviction that pattern-contingent aftereffects such as we had described are inducible in most subjects. Besides using grating stimuli, we extended our experiments to arrays of spots at differing magnifications to see whether spacing-contingent chromatic aftereffects like those of experiment

7.1.1 were also inducible dichoptically. (MacKay and MacKay, 1975a.)

The temporal properties of the McCollough effect established in chapter five are useful as 'finger prints' by means of which to recognise whether such dichoptically induced effects are genuinely akin to the McCollough effect.

Experiment 6.1.1. The time course of decay of dichoptically induced orientation- and spacing-contingent aftereffects

Testing: The apparatus M_1 with test card T_2 or T_3 at 75 cm illuminated at 4 mlm was used for making the pre- and post-exposure measurements. The two eyes were tested alternately, the other eye being confronted meanwhile by a black shutter.

Exposure: The apparatus used for synchronously presenting achromatic patterns to one eye and unpatterned coloured fields to the other has been described fully in chapter 4.1.5. It consisted of a small lamp with red and green movable colour filters set close to one eye, and two projectors with a shutter (E_1) producing achromatic images which were visible by the other. The grating patterns subtended 2.5 cycles/degree. The hexagonal arrays of white spots on a black ground which were used for both exposure and testing subtended 1.8 and 4.8 dots/degree. The luminance of the white areas of the achromatic exposure patterns and of the coloured fields was 8 mlm.

Exposures lasting 15-20 min with a presentation cycle of 6 sec on, 3 sec off were given using gratings, to fifteen subjects and using hexagonal arrays of white dots on a black ground to 10 subjects. Six of the latter were new to dichoptic McCollough-style exposures. In a majority - though by no means all - of the runs the patterns were presented to the left eye and coloured fields to the right.

Results: Table 13 shows the alteration in the verbal reports and in the recorded hue match settings brought about by the dichoptic exposure in the pattern- and colour-stimulated eyes of these subjects.

The verbal reports were considered 'inconclusive' when the subject gave an unchanged report of the colouredness of the parts of the test field-whether the post exposure report was of the 'correct' hues or not.

The decay of the pattern contingent effects was recorded. Figure 24 shows typical results following dichoptic exposure to a) gratings, b) spots, plotted on log/log coordinates with time origin at the end of the exposure. Those results in which the pairing and colour in the aftereffect was the reverse of that in the normal (negative) aftereffect are plotted below the axis. The results of figure 24 may be compared with figure 29b of 7.1.1.1 which shows, for the same subject, the decay of aftereffects induced by presenting red and green gratings or spots. For this subject the level at which the chromatic aftereffects were barely visible was 0.2 cm.

6.1.1.1 Orthogonal gratings

For the eye exposed to colourless gratings the hue settings of 13 of the 15 subjects showed a significant orientation-contingent aftereffect opposite to the normal McCollough effect. The hue recorded for each orientation was the same as that paired with it (in the other eye) during the dichoptic McCollough exposure. With this eye verbal hue naming was reliably consistent with the hue match settings.

For the eye exposed to unpatterned colours the hue settings and verbal reports of 11 of the 15 subjects showed a significant pattern-contingent aftereffect in the same sense as the normal McCollough effect (i.e. as observed when colour and pattern are simultaneously presented

Table 13

PCCAs (verbal and measured) of dichoptic stimulation

Adaptation	Eye tested	PCCA	DA	KB	MF	RH	SH	JJ	DM	DMM	EM	JM	MM	RM	VM	GP	RQ
			Subjects														
(a) Gratings	Pattern-stimulated	Verbal	S	S	S	?	S	S	S	S	S	S	S	S	S	S	S
		Measured	−0·50	−0·55	−0·23	−0·03	−·046	−0·25	−0·04	−0·57	−0·26	−0·32	−0·18	−0·15	−0·36	−0·17	−0·74
(a) Gratings	Colour-stimulated	Verbal	?	C	?	C	C	C	S	C	C	C	C	C	C	C	?
		Measured	−0·19	+0·57	+0·15	+0·12	+0·42	+0·22	+0·28	+0·41	+0·26	+0·03	+0·27	+0·16	+0·72	+0·32	+0·24

Adaptation	Eye tested	PCCA	JB	KB	JC	SH	CJ	SK	DMM	VM	AP	MY
(b) Large + green/ small + red	Pattern-stimulated	Verbal	S	S		?	S	—	S	S	S	S
		Measured	+0·10	−0·05		−0·30	0	+0·05	−0.30	−0·25	−0·30	−0·07
(b) Large + red/ small + green		Verbal	S	?	?	S	S	—	—	S	S	S
		Measured	+0·25	−0·50	+0·10	−0·55	−0·17	−0·20	−·035	−0·20	−0·10	−0·40
(b) Large + green/ small + red	Colour-stimulated	Verbal	C	C		?	C	—	?	C	?	C
		Measured	+0·07	+0·40		+0·20	+1·0	0	+0·25	+0·30	+0·65	+0·50
(b) Large + red/ small + green		Verbal	C	C	?	C	C	—	—	C	C	?
		Measured	−0·07	+0·20	+0·10	+0·10	+0·40	−0·35	+0·56	+0·30	0	+0·05

(a) Orthogonal gratings; (b) hexagonal arrays of large/small dots. Normal PCCAs positive, anomalous PCCAs negative. Readings are averaged over first 5 min.
S, same as hue originally paired with similar pattern.
C, complementary to hue originally paired with similar pattern.
?, no colour or inconclusive.
—, not recorded.

to the same eye). The scatter of the results for this eye was generally larger than for the other. It was noticeable that the sensitivity to colour was reduced by the exposure to alternating red and green light.

The strength of the dichoptically induced aftereffects was in each eye of the order of 1/3-1/10 that of the normal McCollough effect for the same exposure time in the same subject.

Time course. The dichoptically induced aftereffects in each of the two eyes were as long-lasting as normal McCollough effects of the same initial strength. For the five subjects whose aftereffects were large enough to be plotted, as a function of time elapsed from the end of exposure, the results showed no significant departure from the log/log straight line of slope about 0.3 which we had found to fit the normal McCollough effect (MacKay and MacKay, 1974a). The average duration of a visible effect for these 5 subjects was about an hour.

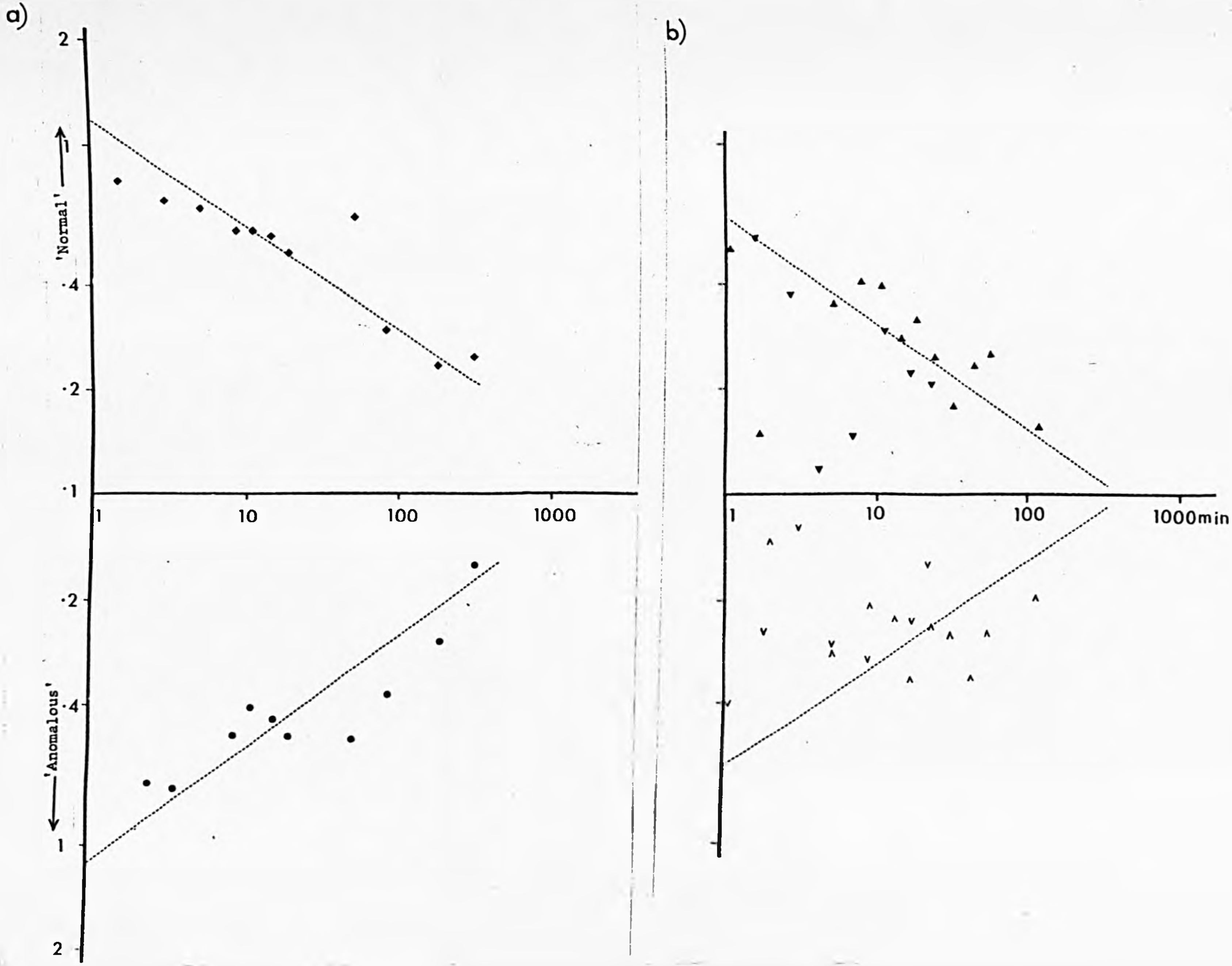
6.1.1.2 Hexagonal dot patterns

The aftereffects, though considerably weaker were generally in the same sense as that found for the orthogonal gratings.

For the eye exposed to colourless patterns most of the measurements and verbal reports showed the 'anomalous' pattern contingent aftereffect - i.e. the hue recorded and reported for each test pattern was the same as that paired with it (in the other eye) during the dichoptic McCollough exposure.

For the eye exposed to unpatterned colours the measured differences in hue settings though weak, mostly showed a 'normal' aftereffect - i.e. each test pattern had the hue opposite to that paired with it (in the other eye) during the dichoptic McCollough exposure.

fig 24



No significant aftereffects in the anomalous direction were reported even under the near 'forced choice'* conditions that were necessary in about 50% of cases.

6.1.1.3 Strength and time course

The strength of the effect with either eye was again of the order of 1/3-1/10 of that obtained in the same subjects by adapting monocularly for the same time to the same patterns in red and green (compare figs. 24 & 7). The aftereffects lasted 7-25 min but were too weak compared with the scatter of the results for the time course of decay to be accurately determined. The rate of decay appeared to be similar to, or somewhat more rapid than, that obtained using gratings. In some subjects the effects were significantly different in strength according as red/green were paired with large/small dots respectively. This bias is possibly related to a separate shortlived effect which is investigated in Appendix I.

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* See 4.3

Figure 24

a) Time course (on log/log scale) of dichoptically-induced chromatic aftereffects of 15 min exposures to gratings in one eye plus colour in other:

◆ eye pre-exposed to unpatterned colours;
● eye pre-exposed to colourless gratings.

b) Ditto for hexagonal arrays of dots in one eye plus colour in other:

▲ eye pre-exposed to unpatterned colours, red paired with large dots;
▼ ditto, green paired with large dots;
∧ eye pre-exposed to colourless dots, red paired with large;
∨ ditto, green paired with large.

6.1.1.4 Conclusion

Orientation-contingent chromatic aftereffects are dichoptically inducible in a high proportion of subjects and have a time course in the normal environment similar to that of the McCollough effect. The after-effects are opposite in the two eyes.

The eye exposed to unpatterned colour sees a 'normal' McCollough effect i.e. the test grating takes a hue complementary to that originally paired with its orientation. The other eye, previously exposed to colour-less pattern, sees what we have referred to as the anomalous McCollough effect, in which the hue seen on each test grating was the same as that previously associated with its orientation.

Similar spacing-contingent chromatic aftereffects have also been dichoptically induced.

How then did it come about that after dichoptic exposure Over et al's (1973) subjects gave as few reports as they did of seeing hues on the test fields? Experiments 6.1.2, 6.1.3 investigate two respects in which their inducing situation differed from ours - luminance of the inducing stimuli and the duration of the on period.* From these I conclude that although no single factor renders the aftereffects unobtainable, non-optimal conditions in one or more respects brought the aftereffects below the detectable level for most of Over et al's subjects (see also 6.1.6).

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* Other obvious factors are the luminance of the test card (see 2. the layout of the test card (see 4.2.1) and intersubject differences (cf. 5.8.1 and table 13 above).

6.1.2 Growth; retention in darkness

Before leaving the temporal aspect of dichoptically induced pattern-contingent aftereffects, mention may perhaps be briefly made of some pilot studies on the growth of these effects and on their behaviour in darkness. These studies reinforce the impression gained from the above experiment that dichoptically induced pattern-contingent chromatic aftereffects are closely related to the ordinary McCollough effect.

Figure 25 shows the growth of the orientation-contingent chromatic aftereffects in the two eyes as a function of exposure time. The dotted line,–included for comparison,–shows the average growth of the McCollough effect (induced by coloured gratings) for the same subject at about the same date, under closely similar conditions of exposure and testing.

The decay of the dichoptically induced aftereffects when light is excluded from both eyes or from one eye for periods of 20 min to several hours has also been investigated. As the effects being studied are not large, the following conclusions are somewhat tentative. Considerable, and possibly total, arrest of decay occurs for both the 'colours' and the 'pattern' eye when the eye is kept in darkness whether the other is receiving light or not. When light is permitted to enter the eye again, decay proceeds at the 'normal' rate ($\beta \doteqdot -\cdot 3$), with time origin at the end of the dark period.

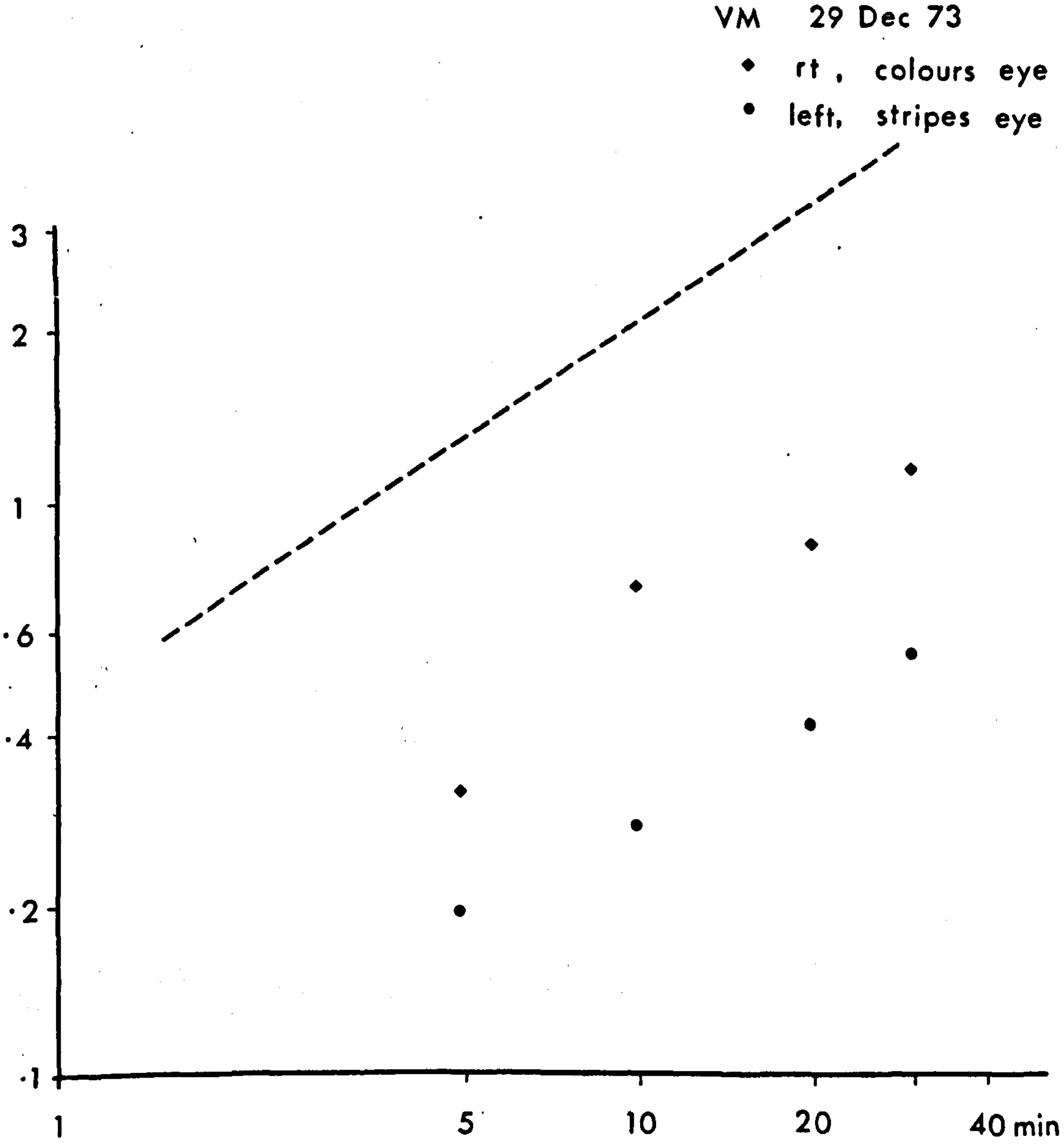


Figure 25: Growth of dichoptically induced orientation-contingent aftereffects.

The magnitudes of the effects induced in the eye exposed to colour ◆, and to pattern ●, plotted on log/log coordinates as a function of exposure duration. Note that the polarity of the aftereffects are opposite in these two eyes though they are both here shown above the axis.

The average growth of the monocularly induced effect in the same subject is included for comparison (dotted). The presentation cycle was in each case 6 sec on 3 sec off.

Experiment 6.1.3 The effect of the luminance of the inducing stimuli upon the strength of the dichoptically induced O.C.C.A.

The luminances of the coloured fields and achromatic gratings presented to the two eyes were separately altered (largely by means of neutral density filters) so as to cover, in a series of runs, the range 1.0 to 2.3 log ft L (0.34-685 cd/m^2). Apparatus and method were otherwise as for the preceding experiment. The same presentation timing (6 sec on, 3 sec off) and duration (15 min) were used throughout the series. The use of left or right eye as the 'colours' or 'grating' eye was randomised across runs.

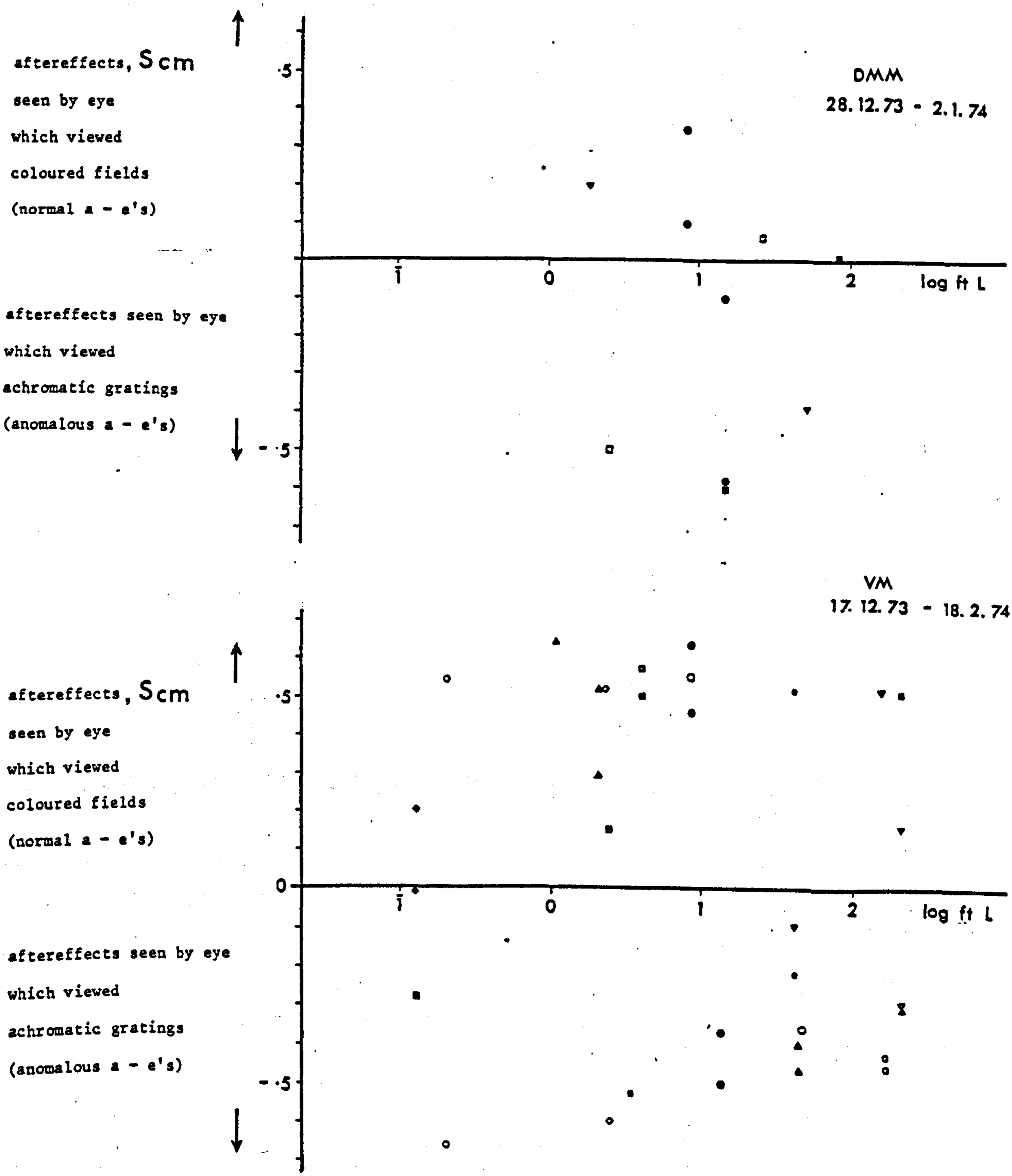
Results: Figure 26 shows, for two subjects, the variation with inducing luminances, of the aftereffects in the colour- and pattern-stimulated eyes. A different symbol is used for each pair of luminances. (The aftereffect magnitudes are the difference between average of the last four readings before exposure and the average of the first four readings after exposure, these readings being made within 2 min of the exposure.)

Findings: The aftereffects in the colour- and the pattern-stimulated eyes were always 'normal' and 'anomalous' respectively. The aftereffects were not very sensitive to inducing luminance. They were strongest for inducing stimuli in the range 0-1.3 log ft L, but were obtainable over a range of 2 or 3 log units. Aftereffect magnitudes were unaffected by differences between the luminances presented to the two eyes - which were as great as 2 log units.

The average luminance used by Over et al. (1973), 18 cd/m^2, fell well within the optimum range.

Figure 26: Initial magnitudes of orientation-contingent aftereffects induced by stimuli of various luminances presented to the two eyes.

Different symbols refer to runs under different conditions



6.1.4 Since Over, Long and Lovegrove (1973) had used very brief 100 msec on periods (in order to avoid interocular rivalry during exposure), it seemed possible that this was the source of divergence between their results and ours. We did not precisely replicate their conditions, for we used on periods of 100 msec separated by off periods of 2 sec, where they had used intermittent presentation of one colour and orientation with a 200 msec cycle for 10 sec followed by 10 sec intermittent presentation of the other colour of stripes. Nevertheless we found that even under our much less promising conditions, aftereffects were still inducible, though at about half the strength obtained on a 6·sec on, 3 sec off cycle.

Experiment 6.1.5 Variants on the dichoptic stimulus

Below, (table 14), are shown diagrammatically the four further variants of the dichoptic situation in which a full McCollough stimulus is presented to one eye and only part of it to the other.*

Subjects were exposed for 15 min to these stimuli using tachistoscopes (E_4, E_5) or the two projectors with shutter (E_1). The gratings subtended 1.9-3.2 cycles/degree. Apparatus M_1 with test figure T_1 was used to make the pre- and post-exposure hue matches.

Results: Table 14 gives the magnitudes of the hue changes induced in each eye of one subject (VM) and also expresses the effect in the left eye as a percentage of that in the right. Negative signs are used for results in which the pairing of colour and orientation in the aftereffect

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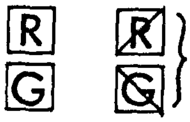
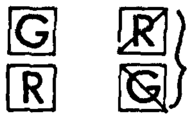
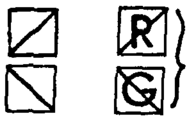
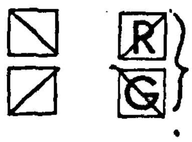
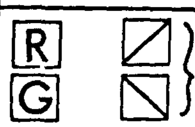
* I am indebted to Keith Bradshaw for the idea for condition d). The reader is referred to his much more exhaustive experiments on all these dichoptic conditions. (Keith Bradshaw, 1978.)

Table 14 Interocular transfer of the McCollough effect under dichoptic exposure conditions

Condition	Stimulus L	Stimulus R	O.C.C.A.s L	O.C.C.A.s R	Left/ Right%	Verbal report on left eye's a-e.
a)			+0.49 +0.44	1.30 1.33	35% approx.	positive transfer
b)			-0.01 +0.02	1.47 1.40	0	no difference between the two parts of test field
c)			-0.43	1.90	23%	definitely opposite in left eye
d)			+0.40	2.60	15%	a-effect is reverse of initial bias and definitely of same pairing as in the exposed eye
e)			+0.38	-0.47		

Two other subjects exposed to condition b) gave barely significant negative transfer.

is the reverse of that in the right eye. Typical results for the simple dichoptic situation of experiment 6.1.1 are also included (e) for comparison.

Findings: The last two columns of table 14 show that 20-30% inter-ocular 'transfer' can occur under dichoptic conditions in which one eye receives the full McCollough stimulus while the other views either colours or pattern. Transfer is positive or negative according as a) the same colours, c) the same orientation of gratings are simultaneously presented in the two eyes. These transferred effects are thus similar in magnitude and in their pairing of colour and orientation to the normal and anomalous dichoptic effects e) induced in the same time using similar stimuli.

Transfer is not greatly impaired when conflicting orientations are simultaneously presented to the two eyes (compare d) with c)), but it is near zero when the colours are complementary (compare b) with a)).

6.1.6 Dichoptic McCollough effects: other authors

Although Over, Long and Lovegrove (1973) denied that the McCollough effect could 'be generated by displaying contour information to one eye and color information to the other', (using condition e) above) other authors have subsequently reported 'interocular generalisation' under conditions a) and c). Keith White (1976, p. 82) presented homogeneous coloured fields to one eye while the other viewed the full McCollough stimulus. Mikaelian (1975, p. 663) presented an achromatic grating to one eye and a coloured grating to the other. Significant normal and 'reversed' McCollough effects were reported respectively under these two conditions.

Though it is possible that the brief exposures used by Over, Long and Lovegrove led to reduced dichoptic aftereffects I am more inclined to think that it was their method of pooling the results under 'left eye' and 'right eye' (rather than under pattern stimulated eye and colour stimulated eye) which obscured the evidence.

6.1.7 Discussion: Interocular transfer of pattern and colour

It is not easy to account simultaneously for the polarity or the magnitudes of the aftereffects in all five of the above cases, a) to e) of experiment 6.1.4. If one summarises the situation, as Over's group have often done (e.g. Over, Long and Lovegrove, 1973), by saying that pattern information transfers binocularly while colour information does not, we have two cases left unaccounted for; the near zero effect in the left eye under conditon b) and the considerable effect in the right eye under condition e). Indeed the results under conditions e), a) and c) show that both colour and pattern information supplied to one eye can influence the aftereffect seen by the other.

In trying to devise a simple explanation for the above results two points seem to stand out:

i) If pattern is already being presented to an eye, the pattern information transferred from the other eye is largely ignored. This is deduced from the smallness of the difference between the magnitudes of the left eye's results under conditions c) and d).

ii) Colour: The difference in polarity of these results is easily explained if we assume that the (complementary) colour information having transferred interocularly combines in each case (c and d) with the pattern information already present. Such an assumption also fits the 'anomalous' results produced under conditions c) and e). In all these cases the transfer – in a complementary colour – is to an eye viewing an achromatic patterned field.

When, however, we turn to the cases (a and b) in which both eyes were presented with coloured fields this complementary colour story seems to break down, for it is only insofar as the two eye channels have colour information in common that the pattern information transfers.

There is obviously scope here for further experimental elucidation.

To explain the aftereffect in the eye which has viewed achromatic gratings during dichoptic presentation of the McCollough stimuli, it might be supposed that a central colour normalising mechanism shifts the zero for 'whiteness' in both eyes in the same direction. This would have the effect of emphasising the complementary colour in the eye exposed to pattern so that the patterns are taken to be greenish or reddish according as red or green light floods the other eye. Such a normaliser might be arranged so as to globally affect the entire input to the other eye, or it might operate for each hemiretina separately or yet more locally. In the next experiment the unanimity of the colour message across the retina and then within each hemisphere is disturbed while keeping the pairing of colour and orientation unchanged.

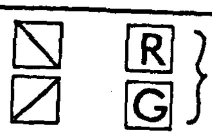
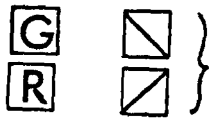
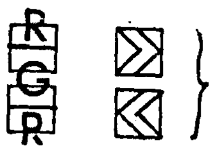
Experiment 6.1.7.1 Global or local transference of colour information in the dichoptic effect?

The aftereffect strengths resulting from three exposure conditions were compared (M_1 and test card T_2 at 46 cm). All three conditions involved dichoptic presentation of achromatic gratings and colour, but in the first the fields seen by the two eyes were of one colour or orientation throughout while in the second the fields were divided vertically and in the third horizontally. The divided fields were produced by slicing the full field colour filters and grating patterns along a midline parallel to one side and pairing them up again, so that two colours or two orientations were simultaneously visible by each eye. For example, in Table 15 we see that on the 14 June 1976 the left eye was presented with red above and green below alternating every ½ sec with green above, red below, while the right eye viewed, alternately, the two 90° chevron patterns of 1.9 cycles/degree. During exposure the subject ran his eye along the divide between the two half fields (or round a fixation circle in the case of the undivided fields).

The full field and divided field stimuli were presented by tachistoscopes E_5 and E_4 respectively. The presentation cycles were different for the two tachistoscopes (10 sec on, 10 sec off for E_5; ½ sec on, 0 sec off for E_4) but the runs were in all other respects made as similar as possible.

Results: Table 15 shows the magnitudes of the alteration in orientation-contingent chromatic biasses resulting from 15 min dichoptic exposures under the three conditions. The pairings of colour and orientation of

Table 15 The results are called positive in which a pink aftereffect is seen on right oblique gratings.

Subject	Date	Exposure condition Left	Exposure condition Right	Duration (minutes)	Aftereffect Left	Aftereffect Right
full field						
VM	4 Oct. 1976			15	-0.20	+0.63
VM	5 Oct. 1976			15	-0.45	+0.50
vertically divided field						
VM	17 June 1976			15	-0.60	+0.20
ECM	17 June 1976			15	-0.09	+0.38
horizontally divided field						
VM	14 June 1976			15	+0.45	-0.47
DMM	14 June 1976			15	+0.20	-0.37

aftereffects are in every case in accord with the conclusions drawn in experiment 6.1.1.1 . ECM saw no hues on the test card using her left eye. In every other case the verbal reports of the hues seen tallied with the measurements.

Findings: Dichoptic aftereffects were induced by both the vertically and the horizontally split fields as readily as by full field stimuli.

Conclusion: In the McCollough effect the communication of colour information between the monocular channels does not take place globally or even on the basis of the average coloured input to a hemisphere, but on a more localised, possibly point by point, basis.

A further dichoptic experiment concerning the transference of the pattern information was unfortunately without outcome. It was directed to the question as to whether it is the pattern or its inverse which becomes paired with the colour input to the other eye. A dot pattern and its photographic negative were presented to one eye, the red and green unpatterned fields to the other. It had been found (see chapter 7.1.1.3) that a chromatic aftereffect contingent upon polarity of the contrast is visible on test figure T_7 after presentation of the above pattern and colour stimuli to the same eye. If the corresponding effect occurred dichoptically it was too small to be detectable.

6.2 Interocular Transfer of the McCollough effect

In view of the degree of interocular linkage demonstrated by the dichoptic results above, it seemed strange that the McCollough effect should not transfer to an unexposed eye. McCollough (1965b) and Murch (1972) had reported that none occurred after up to 16 min of exposure. I have investigated transfer under the conditions which they used (one eye covered during exposure and the other during testing) and also under three further conditions (experiments 6.2.1.2 to 6.2.1.4).

Experiment 6.2.1 To investigate interocular transfer of the McCollough effect:

6.2.1.1 with all light excluded from the unexposed eye during the McCollough exposure

The apparatus M_1 with test field T_2 at 75 cm was used to make the pre- and post-exposure hue matches. These were performed by each eye in a darkened room with a black shutter close in front of the other eye. The post-exposure hue settings using the unexposed 'transfer' eye were always completed and a verbal report invited before the subject was allowed to view the test card using his exposed eye.

The exposure was for 15-20 min to red and green oblique orthogonal gratings of 2.5 cycles/degree, all light being meanwhile excluded from the other eye by means of an eye patch and the subject's cupped hand.

Results: Table 16 shows, for 7 subjects, the magnitude of the effect induced in the exposed eye and the alteration in the readings made using the 'transfer' eye. Biasses of below 0.2 or 0.3 are generally not visible.

Only half the subjects (CF, JI, DMM and VM) gave different verbal reports of hues seen before and after exposure, and they were for the most part hesitant. VM saw a hue change in fewer than half of 16 runs. Nevertheless, such hues as were reported were in accord with the readings.

Table 16 Interocular transfer of the McCollough effect to a covered eye

Subject	Sex	Time	Date	Exposed eye			Covered eye			Percentage transfer
				Condition	Duration (min)	McC. a-e (Scm)	Pre-exposure bias	Post-exposure bias	Change in bias	
CF	F	-	8.12.72	R	15	7*	-0.27	+0.34	+0.61	+9.0
VM	F	10.10 am	4.7.73	R	20	4.4	+0.10	+0.68	+0.58	+13.0
		11.01 am	5.7.73	R	20	4.4	0	+0.11	+0.11	+2.5
		3.33 pm	5.7.73	R	20	3.9	+0.07	+0.25	+0.18	+5.0
		3.32 pm	6.7.73	R	10	1.5	+0.09	+0.19	+0.10	+7.0
		3.52 pm	6.7.73	R	10	0.7	+0.03	+0.24	+0.20	+30.0
		4.15 pm	6.7.73	R	20	4.2	-0.23	+0.10	+0.33	+9.0
AMH	F	9.47 am	5.7.73	R	20	2.3	-0.30	+0.07	+0.37	+16.0
		4.35 pm	5.7.73	R	20	3.9	+0.15	+0.13	-0.02	-0.5
BM	F	1.48 pm	11.7.73	R	20	2.5	+0.03	+0.34	+0.30	+12.0
MY	F	4.35 pm		L	15	2.2	-0.11	+0.01	+0.12	+5.0
DMM	M	11.55 am	13.8.73	R	20	3.55	+0.03	+0.28	+0.25	+7.0
JI	F	2.30 pm	13.5.75	L	20	1.2	+0.05	+0.24	+0.19	+5.0

* the calibration of the plotter was different before 23 June 1973.

Results are called positive when they have the same pairing of colour and orientation as the aftereffect in the exposed eye.

Conclusion: Although the aftereffect in the 'covered' eye is barely visible, the readings from the above 7 subjects suggest that positive transfer to a covered eye does take place and that it has about 8% of the strength of the aftereffect in the exposed eye.

In the next three experiments, the reports of other authors (Baker, May and Mash, 1976 and Mikaelian, 1975b) led one to expect larger and more visible transfer than in the above experiment, but as this was not found the experiments are only briefly reported.

6.2.1.2 White light entering the 'transfer' eye during the McCollough exposure

An unpatterned white field of 11-17 cd/m^2 was presented to the 'transfer' eye either continuously or switched on and off synchronously with the presentation of the coloured (17 cd/m^2) gratings to the other eye. In some runs a fine fixation circle was placed in the middle of the white field to ensure that the input to the transfer eye was not suppressed.

Testing of the 'transfer' eye in apparatus M_1 was performed both with and without a light input (11 cd/m^2) to the other eye.

Results: A barely significant positive transfer was revealed by the readings under both test conditions. This hue change was not visible to the subject.

Conclusion: Transfer was no larger than under the condition where no light entered the unexposed eye during the McCollough exposure.

6.2.1.3 A steroscopic view during both exposure and testing

In 1976 Baker, May and Mash reported that when viewing conditions were such as to ensure that neither eye's input was suppressed during induction or testing 'it is about as easy to induce McCollough effects interocularly as monocularly'. They used a stereoscope to present a $25^\circ \times 25^\circ$ view of a shelf and desk top supporting books and other predominantly vertical and horizontal objects.

A smaller central region ($7^\circ \times 10^\circ$) 'embedded' in this view could contain monocularly presented views of the inducing gratings, test gratings or a plain white field. After 10 minutes' exposure to coloured vertical and horizontal gratings 10 out of 11 subjects reported positive transfer (3 of them under forced choice conditions). As a routine part of the test procedure all subjects were 'told to scan the background' before making their forced choice judgement as to which half of the test field appeared either pinkish or greenish. This change of fixation will, of course have used, in testing, parts of the retina which had previously been exposed to the coloured book spines. The authors explain that the manoeuvre was recommended to the subjects because 'we . . . had sometimes observed that the McCollough colors would appear suddenly as both eyes became active . . . looking into the background'.

To replicate the essentials (though not the details) of this experiment the two eyes were provided with half-silvered mirrors in which they viewed respectively the inducing gratings and the test field T_2 of apparatus M_1 against a common binocular view of a black velvet disc which formed part of an elaborate three dimensional object* whose purpose was to ensure that neither eye's input was suppressed. The inducing gratings, test card and a binocularly seen fixation wire were all at exactly the same distance (96 cm) from the subject's eyes. Each of the monocular views could be cut off by a black card.

The scatter in the hue matches was very small but no interocular transfer of the McCollough effect was measured or perceived after a 20 minutes' McCollough exposure though the effect in the exposed eye was strong.

6.2.1.4 "Interocular generalisation" after exposure?

Mikaelian (1975b) has reported that "interocular generalisation" of the McCollough effect can occur after exposure under the following conditions. One eye was exposed to the coloured McCollough gratings for 4 min, then both eyes viewed the achromatic test figure for 2-5 min and then the two eyes were tested separately. Of Mikaelian's 27 subjects, 24 then reported seeing chromatic effects using each eye. The effects in the eye which had not been exposed to the McCollough stimuli were 'weak'. Subjects differed as to which colouring they saw with this eye on the

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* The black screen was not only surrounded by a circular frame of random noise with an outer rim displaced 2" further from the subject, but also supported about 100 small white polystyrene dots at distances of 0-2" from its surface. A wire along which the subject continuously ran his eye was fixed 1" in front of the velvet background, and the subject gave his attention throughout the experiment to the seeing of the scene in three dimensions. The whole three dimensional object was illuminated by two lamps and in monocular view lacked any appearance of depth.
In practice it was found that despite all these precautions suppression of a kind did take place. But it was suppression of a part and not of the whole of the eye's input. When the coloured gratings were presented against the black velvet field the gratings were not seen either at or for a small distance (about $1/20^{o}$) around each white dot.

vertical and horizontal stripes; for 14 subjects the hues were opposite in the two eyes and for 10 they were the same.

To replicate these conditions, 4 subjects who have medium to large McCollough sensitivity were exposed monocularly (L eye) for 20 min using the two projectors E_1 and oblique gratings of 2.2 cycles/degree. For two subjects (KU, JI) all light was excluded from the 'transfer' eye during the McCollough exposure, for two the inducing (though not the test) conditions of the preceding experiment (6.1.2.3) were employed. The orientation-contingent chromatic effects in both eyes were measured before and after the McCollough exposure using apparatus M_1 with test card T_2. The subjects then viewed the test card T_2 binocularly for over 5 minutes and made further monocular hue match settings using first the 'transfer' eye and making a verbal report on hues seen using it. (During the binocular viewing of the test card the McCollough hues became almost invisible. Shutting the eyes for half a minute revived the colours seen binocularly.)

Results: Table 17 shows the orientation-contingent chromatic effects in both eyes before and after the viewing of the test card. Aftereffects of 0.2 were almost invisible and changes of below 0.2 are not significant.

The verbal reports made using the right ('transfer') eye before and after the viewing of the achromatic gratings were as follows:

KU before: no difference, slightly pink on right oblique;
after: no difference, very slightly pink on right oblique.

JI before: slightly pink on left oblique or no difference;
after: slightly pink on left oblique,–no difference or even green on left oblique.

VM before: very slightly pink on right oblique;
after: both parts of test field orangey pink; right oblique yellower.

DMM before: small green effect on left oblique;
after: 'very strong impression of left oblique green' immediately after viewing the test card but one minute later 'no colour difference at all'.

Table 17 Orientation-contingent chromatic effects (O.C.C.E.s) in the two eyes before and after viewing achromatic gratings binocularly

Subject	Date	Stimulus	Duration (min)	Before		Time viewing test card (min)	After		Change in O.C.C.E. in Right eye (resulting from the viewing of test card)
				L O.C.C.E.	R O.C.C.E.		L O.C.C.E.	R O.C.C.E.	
KU	2.5.76		20	+1.82	-0.24	5	1.08	-0.12	+0.12
JI	13.5.76		20	+4.28	+0.15	6	3.10	+0.21	+0.07
VM	24.5.76		18	+3.27	+0.01	9.7	2.44	-0.03	-0.04
DMM	24.5.76		20	+2.70	+0.33	5	+2.00	+0.21	-0.12

(Positive values are given to those orientation-contingent chromatic effects which have the same pairing of colour and orientation as the aftereffect in the exposed eye.)

Findings: The measurements on the Right eye show no significant alteration as a result of viewing the test card binocularly. The verbal reports also reveal no lasting or convincing transfer either negative or positive. They do, however, suggest that the viewing of the test card produced a very brief enhancement of the perception of such bias as was already present in the 'unexposed' eye.

Conclusion: There seems insufficient reason to interpret Mikaelian's report of an alteration in the appearance of the test gratings following binocular viewing as evidence of interocular transfer (either positive or negative) of the McCollough effect.

6.2.1.5 Summary: Interocular transfer

Transfer of the McCollough effect to a covered eye occurs but so weakly as to be generally not visible. The transfer is positive but below 10% of the strength of the effect induced in the exposed eye.

The degree of transfer is not noticeably increased either by a) having a light input to both eyes, or b) ensuring that neither eye's input is suppressed during exposure and/or testing. Nor is it increased by allowing the two eyes after exposure to view achromatic gratings binocularly.

6.3 Binocularly observable McCollough aftereffects

In 1976 Vidyasagar elegantly showed that there is a binocular ingredient in the McCollough effect. He used a presentation cycle which would, if there were no binocular interaction, have induced no nett McCollough aftereffect observable by each eye singly, or both eyes jointly. This cycle had three parts of equal durations, separated by dark intervals; first, a binocular presentation of McCollough stimuli having a particular pairing of colour and orientation, then a monocular presentation, first to one eye and then the other, of the reversed pairing. At the end of 30 min when the test field was viewed binocularly, a small aftereffect appropriate to the binocular part of the exposure was seen. And monocularly, curiously enough, small aftereffects of the opposite polarity were also seen.*

Vidyasagar's discovery put me in mind of a finding which I had laid on one side in 1973 (figure 28a) as needing a suitable control experiment. After ordinary binocular exposure to a McCollough stimulus, binocular viewing of the test card evinced slightly stronger aftereffects (both measured and reported) than monocular viewing. But without a control experiment there was insufficient reason to ascribe this difference to the McCollough mechanism. At the low test intensities used (11 cd/m^2) the test figure looks considerably brighter when observed by two eyes than with one (cf. Piper, 1903, mentioned by Helmholtz, p. 530), so that it seemed

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* I have replicated Vidyasagar's findings and measured these binocular and monocular effects on three occasions in one subject and find them to be approximately 20% of the McCollough effect produced in the equivalent time (10 min) by a normal McCollough exposure. Though small, they seemed to be, if anything, even more long lasting than ordinary McCollough effects of the same magnitude.

possible that similar enhancements of colour perceptions occurred when using two eyes. The control experiments which show that the McCollough mechanism is implicated in the above observation are described below.

Experiment 6.3.1 Binocular interactions in the McCollough effect

In every run, identical monocular stimuli were presented to the two eyes. The variable was the relative timing of the presentation of the stimuli to right and left eyes. The aftereffects were measured both monocularly and binocularly.

Apparatus and Method: Red and green gratings of 3.2 cycles/degree at $+45^{o}$ and -45^{o} to the vertical were presented to left and right eyes by a tachistoscope (E_5). A presentation cycle of 9 sec on, 9 sec off, and exposure duration of 19-20 min were used throughout the main* runs of figure 27 a . The coloured patterns seen by one eye were presented either, A, in phase with those seen by the other eye; B, 9 sec behind, i.e. a quarter cycle out of phase; or C, 18 sec behind, i.e. half a cycle out of phase. These conditions are diagrammatically represented at the head of figure 27 . The subscripts A_1 and A_2 are used to distinguish conditions in which: A_1, the two eyes viewed a single pair of coloured gratings directly (on a screen or over the tops of the tachistoscope mirrors) and A_2, the tachistoscope was used normally with each eye viewing via mirrors a separate pair of (matched) coloured gratings.

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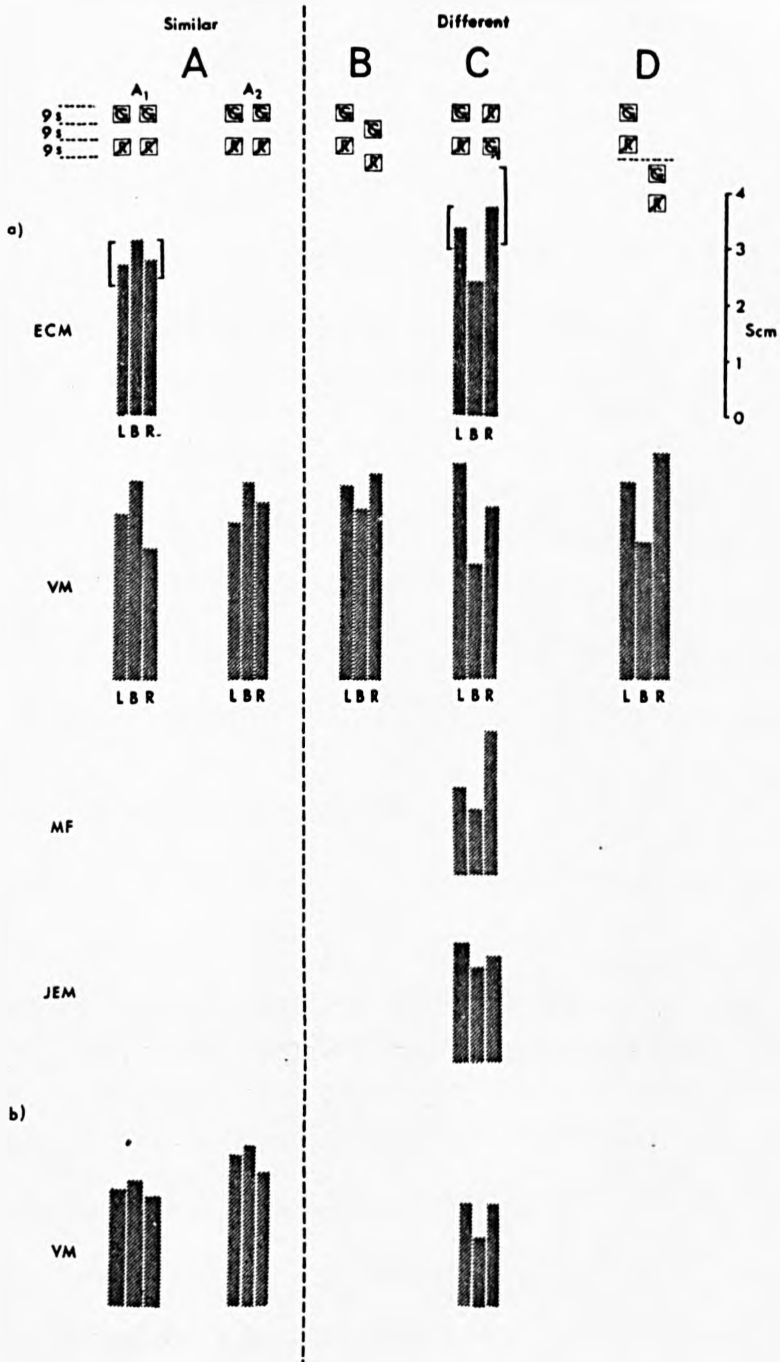
* For the runs on VM in figure 27 b and figure 28 a there were slight differences in various factors such as the time which elapsed before the first readings were taken, and the duration and spatial frequency of the McCollough stimuli. These results are, however, included for within run comparison of the magnitudes of the binocular and monocular aftereffects.

Figure 27 The strength of the McCollough aftereffects

The strength of the McCollough aftereffects seen monocularly and binocularly following exposure of the left and right eyes to stimuli which were:



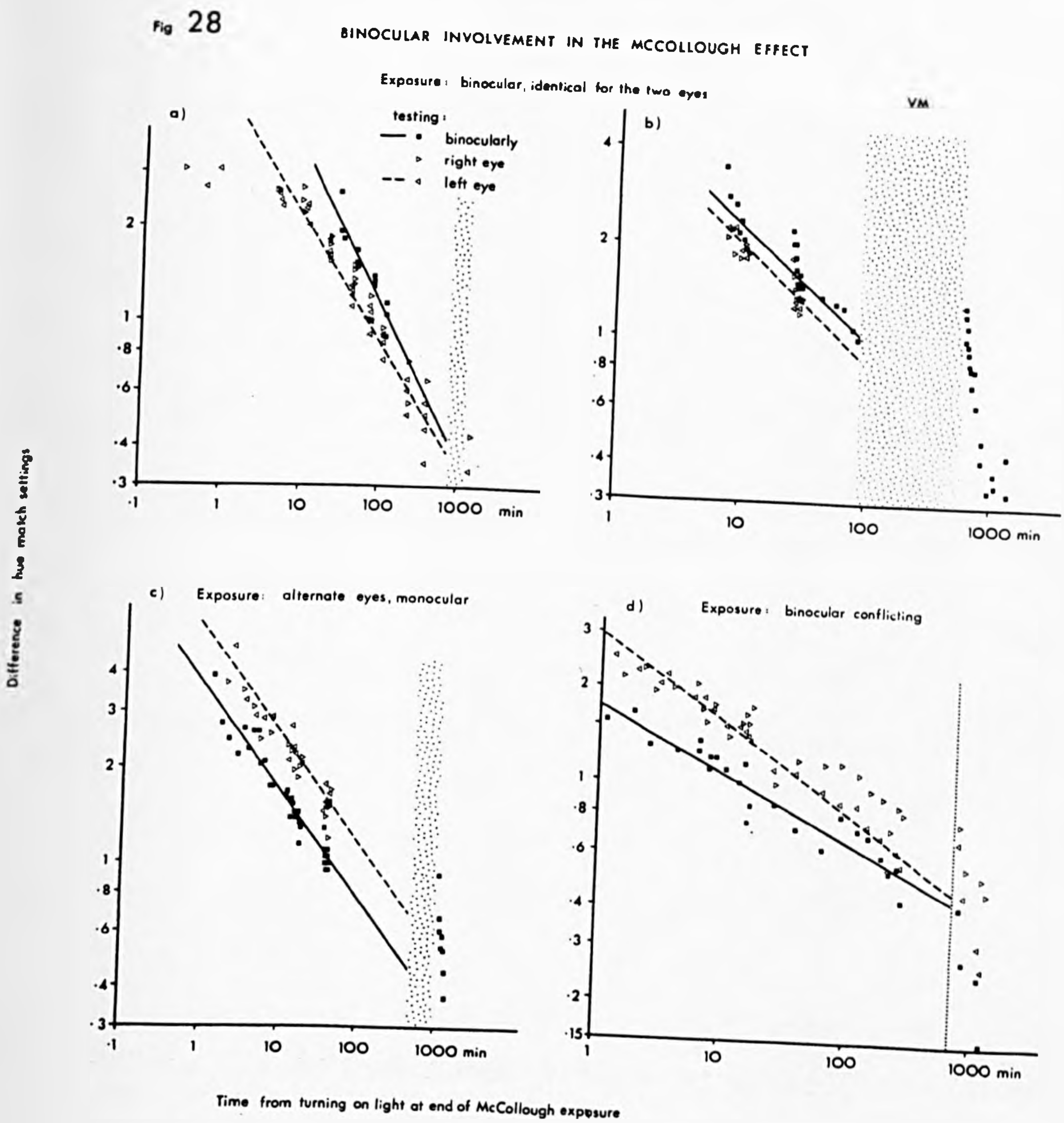
Under a further condition, D, the right eye was exposed for 20 min and then the left (total time 40 min), the unexposed eye being covered by a black patch during each monocular exposure.

The apparatus M_1 with test field T_2 at 94 cm was used for making the pre- and post-exposure measurements. Since the aftereffects decay during the measuring session, the measurements using both eyes and one eye were systematically alternated (both; left; both; right; etc.) four times. Before making the above measurements the subject viewed a large ($60^o \times 60^0$), plain white card at 0.5 log ft L for one minute beginning close after the end of the exposure. Often a second batch of readings was made in the same fashion after 5-7 min had elapsed. When he had finished making the hue match settings the subject was asked to judge whether he saw any difference in the appearance of the test figure when he alternately viewed it using one and using two eyes.

Results: Figure 27 shows the average magnitudes of the aftereffects measured binocularly and monocularly for four subjects under the above conditions. The error bars indicate the standard deviation of the difference between successive monoptic and binocular readings.

Figure 28 shows for one subject the decay of the binocular and monocular effects induced by exposure conditions a) A_1, b) A_2, c) B, d) C. The exposure conditions are specified in detail in Table 18 and the subsequent log/log decay slopes, β, given. Decay took place in a normal laboratory environment at a) ordinary luminance levels, b) c) d), a steady luminance of 11 cd/m^2. Night time, (shown speckled) fell between 100 and 1000 min.

In figure 28 every reading taken has been plotted (without averaging)



The decay of the aftereffects observed binocularly (filled squares, solid lines), and monocularly (unfilled symbols, dotted lines) following McCollough 20 min exposures during which the left and right eyes viewed:

a) the same stimuli on a screen
b) identical stimuli presented simultaneously by a tachistoscope
c) stimuli presented alternately to each eye (1/4 cycle out of phase, see text)
d) stimuli presented so as to conflict in the two eyes (½ cycle out of phase).

Log/log plots. The scales on the abscissae of the various graphs differ. The slopes, β, of the solid and dotted lines and particulars of the exposures are given in Table 18

Subject: VM	Exposure Conditions						Slopes, β, of log/log plots of Figure 28		
Figure	Stimulus	Binocularity	Presentation cycle	Spatial frequency	Date	Time	Binocular	Left	Right
a)		in phase (simultaneously identical to left and right)	10 sec on, 4 sec off	2.2 c/degree	8.1.73	9.30-50 am	-0.49	-0.33	-0.27
b)		in phase (simultaneously similar to left and right)	9 sec on, 9 sec off	3.2 c/degree	14.2.77	9.27-47 pm	-0.36	-0.38	-0.30
c)		1/4 cycle out of phase (alternate monocular exposures)	9 sec on, 9 sec off	3.2 c/degree	9.12.76	11.56-12.16	-0.21	-0.29	-0.20
d)		½ cycle out of phase (conflicting)	9 sec on, 9 sec off	3.2 c/degree	17.3.77	2.20-40 pm	-0.33	-0.34	-0.31

Table 18 Decay of the aftereffects measured binocularly and monocularly following concurring and conflicting McCollough exposures of the left and right eyes

to facilitate comparison of the standard deviation of the readings with the separation between the binocular and monocular readings.

Findings: When the two eyes received concurring inputs during McCollough exposure the aftereffect measured binocularly was larger than that measured monocularly. The binocular measurements were some 14-33% larger than the monocular under both conditions A_1 and A_2.

Under all three conditions (C, B, D)where the two eyes received non-identical inputs, the binocularly measured aftereffects were smaller than those measured monocularly. Investigations to date have not revealed any systematic differences between the aftereffects produced under these three conditions. The discrepancy between binocular and monocular readings is in each case in the range 23-46%.

In every run the difference between the monocular and the binocular readings is significant as can be seen from the standard deviations indicated in figure 27and the graphs of figure 28 .

Following the exposures to concurring stimuli, the subject's verbal reports agreed with the measurements. They were always that slightly stronger hues were seen binocularly than monocularly and that for the other three conditions in which the two eyes had received different inputs at every moment, weaker effects were seen using two eyes than using one.

The subsequent batches of readings of figure 28 suggest that the decay courses of the binocularly and monocularly seen effects are similar. There are signs in figure 27a that the binocular ingredient begins to decay only when light is allowed simultaneously to enter the two eyes (for the first 30 min testing was monocular in a dark room). The monocular rates of decay do not differ systematically (Table 18) under the various conditions (cf. also chapter 5.1).

Comparisons across the carefully matched groups of runs of ECM and VM suggest that the magnitude of the monocular effects is either the same irrespective of the binocular conditions or perhaps slightly smaller for the concurring condition than for the others.

Conclusion: When the two eyes have been exposed simultaneously to the same McCollough stimuli the aftereffect seen binocularly is about 22% larger than that seen monocularly. When the two eyes have been exposed to the same McCollough stimuli but not simultaneously the aftereffect seen binocularly is about 33% smaller than that seen monocularly.

Discussion: These results suggest there is not only a 'positive' binocular McCollough effect (of which Vidyasagar's experiment had already provided evidence), but also a similar, larger 'negative' binocular effect which is induced whenever the McCollough inputs to the two eyes differ.

6.4 Conclusion: Interocular linkages in the McCollough effect

Orientation-contingent chromatic aftereffects (OCCAs), though largely monocular are not wholly confined to the monocular channel. OCCAs visible monocularly have been induced by dichoptic exposures. Binocular OCCAs are revealed by the difference between the OCCAs seen binocularly and monocularly - a difference which can be either positive or negative according as the stimuli presented to the two eyes concur or differ during binocular McCollough exposure. Transfer of the McCollough effect, though not visible by many subjects, takes place weakly to a covered eye. The approximate strengths of these effects compared with that of the monocular McCollough effect (induced by comparable stimuli in the same exposure time) are

dichoptic	25%
binocular 'positive'	22%
binocular 'negative'	33%
transfer	8%

The course of decay of all these effects is similar to that of the monocular effect.

Chapter 7 Essential Features of the McCollough Stimulus

We have seen in the introductory chapters that the McCollough effect is a chromatic aftereffect generated by, and visible only in the close vicinity of dark/light borders. It has been shown that the strength of the hues seen depends upon the orientation and also upon the spacing of the edges* (1.5, 1.6).

The present chapter seeks to elucidate those minimal ingredients of the inducing and test stimuli which are essential for the production of this type of chromatic aftereffect. The main aspects investigated are: spacing devoid of oriented edges; edges devoid of spatial repetition; edges devoid of difference in luminous intensity; and colour without a real difference in input at the primary receptors.

7.1 Spacing or texture of the pattern elements

Previous investigations of the spatial frequency dependent aspects of the McCollough effect (1.6) had all used gratings as stimuli. To find out whether long oriented edges were an essential ingredient of the McCollough stimulus, my husband and I selected stimuli for both exposure and testing which were devoid of straight edges yet still possessed average spacing of dark/light borders.

Experiment 7.1.1 Chromatic aftereffects contingent upon pattern magnification

The methods of experiment 5.1 were employed but using patterns of dots and random noise in place of gratings. Apparatus M_1 with test figures

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* And upon their polarity of contrast also if we include the prism aftereffect as a related phenomenon (1.2).

T_3, T_4, T_5, T_6 at 65 cm were used for making pre- and post-exposure hue matches. The Braun projector (E_2) was used to present alternately, for 10 sec apiece, two slides of a regular hexagonal array of black (or white) spots at magnifications differing by a factor of 2.5. When viewed by the subject from 97 cm these patterns subtended $17^{\circ} \times 17^{\circ}$ and the dots 1.8 and 4.6 cycles/degree. By means of movable red and green filters in front of the subject's eyes the pairing of magnification and colour could be altered in each eye separately.

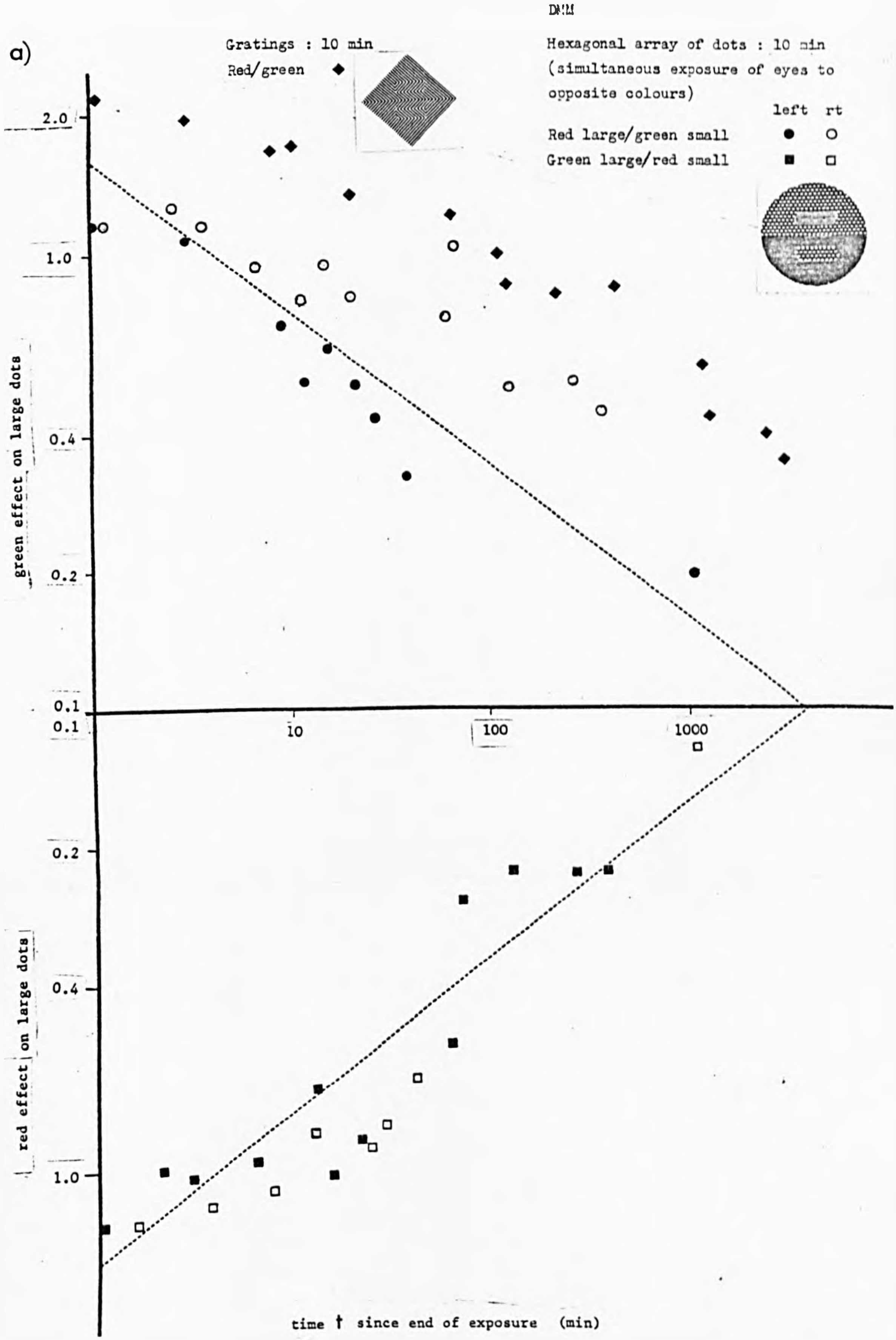
7.1.1.1 Time constants

The inducing stimuli were coloured dots of 1.8 and 4.6 cycles/degree on a black ground, and the corresponding test card (T_3) was employed in making hue matches to the aftereffects.

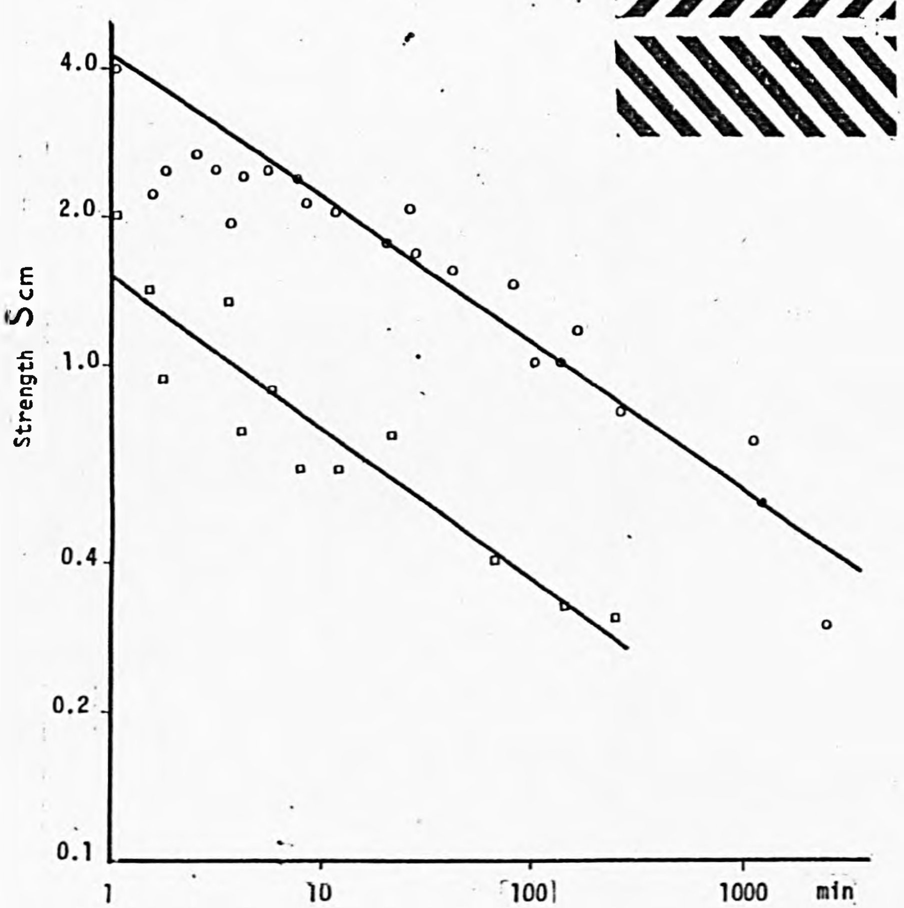
As in experiment 5.1, groups of measurements were made at various times after the end of the exposure, with ordinary life intervening. As in experiment 5.8.1, the inducing exposure was in some runs briefly interrupted to obtain a plot of the growth of the aftereffect against exposure time.

Results: Figure 29a and c, and figure 30 (filled symbols) show typical plots for the decay and growth respectively of the magnification contingent chromatic aftereffects. For the runs of figure 29 a and c the left and right eyes were simultaneously exposed to opposite pairings of colour and magnification (at 6 sec on, 3 off and 13 sec on, 4 sec off respectively for VM and DMM). Figure 29 b and the solid line of figure 29 a are included for comparison; they show in the same subjects the decay of the chromatic aftereffects induced using gratings of 2.5 cycles/degree. The solid and dotted lines all have a slope of 0.31. The dotted line of figure 30, which is similarly included for

Figure 29: Decay of Pattern-contingent chromatic aftereffects



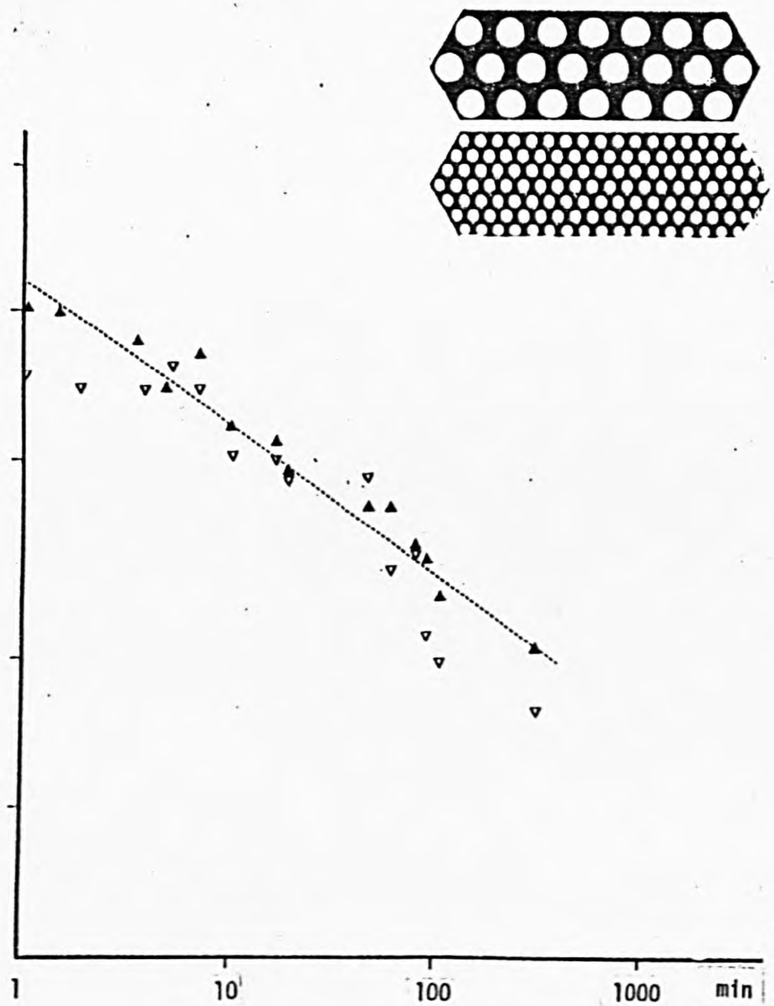
b)



□ red and green gratings: 5 min 6 Sept 73

○ red and green gratings: 15 min 11 Sept 73

c)



▲ dots, red large/green small: 20 min
▽ dots, green large/red small: 20 min
2 March 1974

fig 30

VM 10 Sept 73

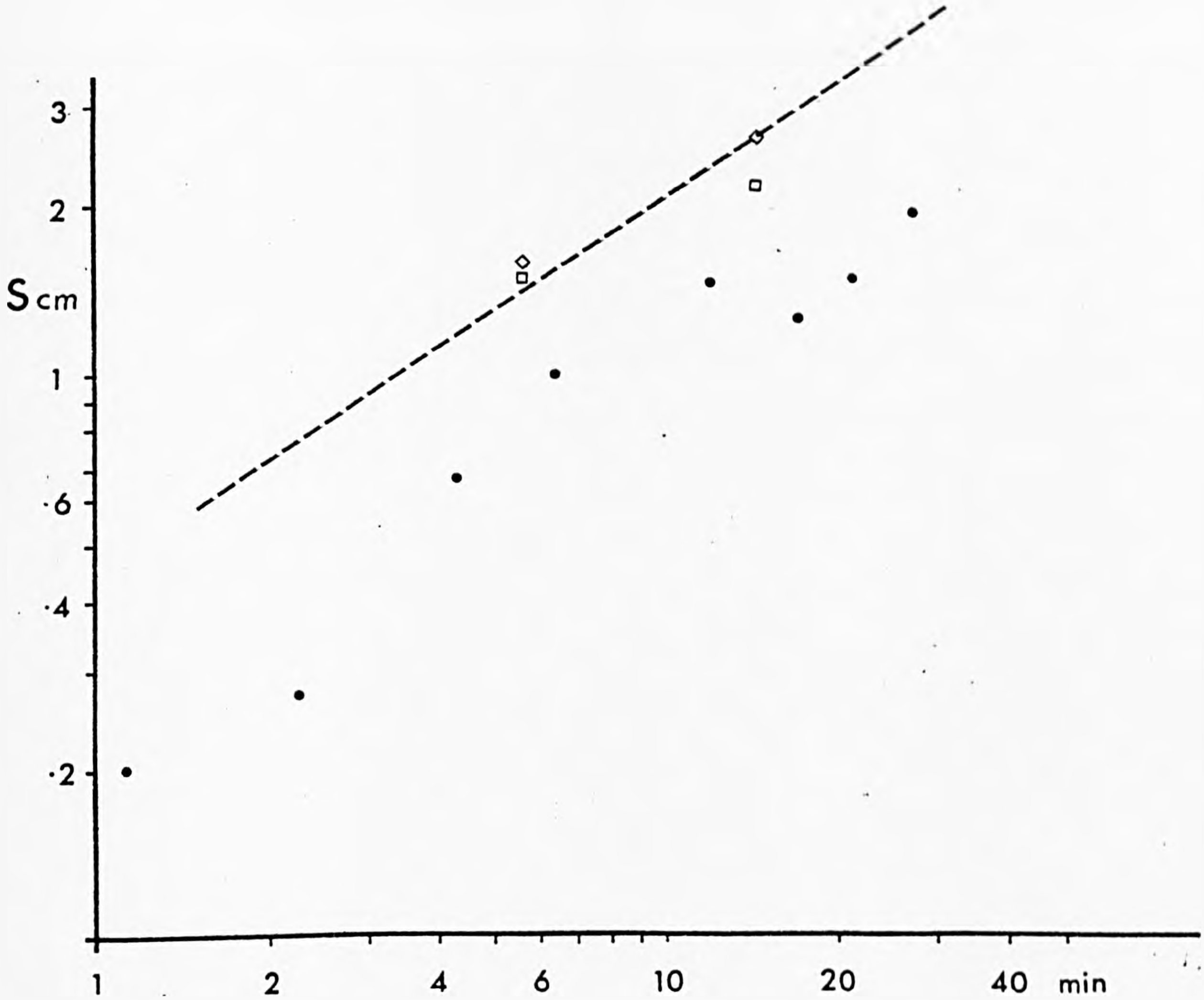


Figure 30 Comparison of the Growth of the Pattern-contingent chromatic after effects induced by:

● regular hexagonal arrays of large red dots and small green dots
◇, □ red and green gratings.

The dotted line represents the average of several runs; the square symbols were measurements made during a similar exposure to gratings which immediately followed the exposure to coloured dots.

Log/log plots of after effect strength against cumulative total duration of exposure.

comparison, is the average of several runs on the same subject using gratings and has a slope of +0.66. The unfilled symbols of figure 30 relate to an exposure to coloured gratings which immediately followed the 35 min exposure to spots.

Figure 31 shows the decay of a magnification-contingent chromatic aftereffect (monocularly) induced 3 min before a night's sleep. With time origin at the end of the exposure, the following day's decay has a log/log slope at least five times as large as that for the day of exposure, but with time origin at the time of waking on the second day the second day's slope becomes 0.19.

Findings: Strong chromatic aftereffects contingent upon pattern magnification were observed using arrays of spots to induce and detect the effects. Their strength was about 57% of that of the McCollough effect induced by orthogonal gratings in the same time. The time constants for growth and decay were highly similar to those for the McCollough effect; decay was arrested by darkness There was a tendency, in each of five subjects, to see larger and longer-lasting aftereffects after exposure to red large dots and green small dots than after exposure to the reversed pairing. For two of five subjects the initial aftereffects differed by a factor of two but for the other three the difference between the aftereffects under the two conditions was below 20%. This bias is in the same direction as the tendency to see finer patterns as pinker, which many subjects evince in the absence of any adaptation.

Conclusion: Strong and long-lasting chromatic aftereffects contingent upon pattern can be induced using regularly arranged coloured dots.

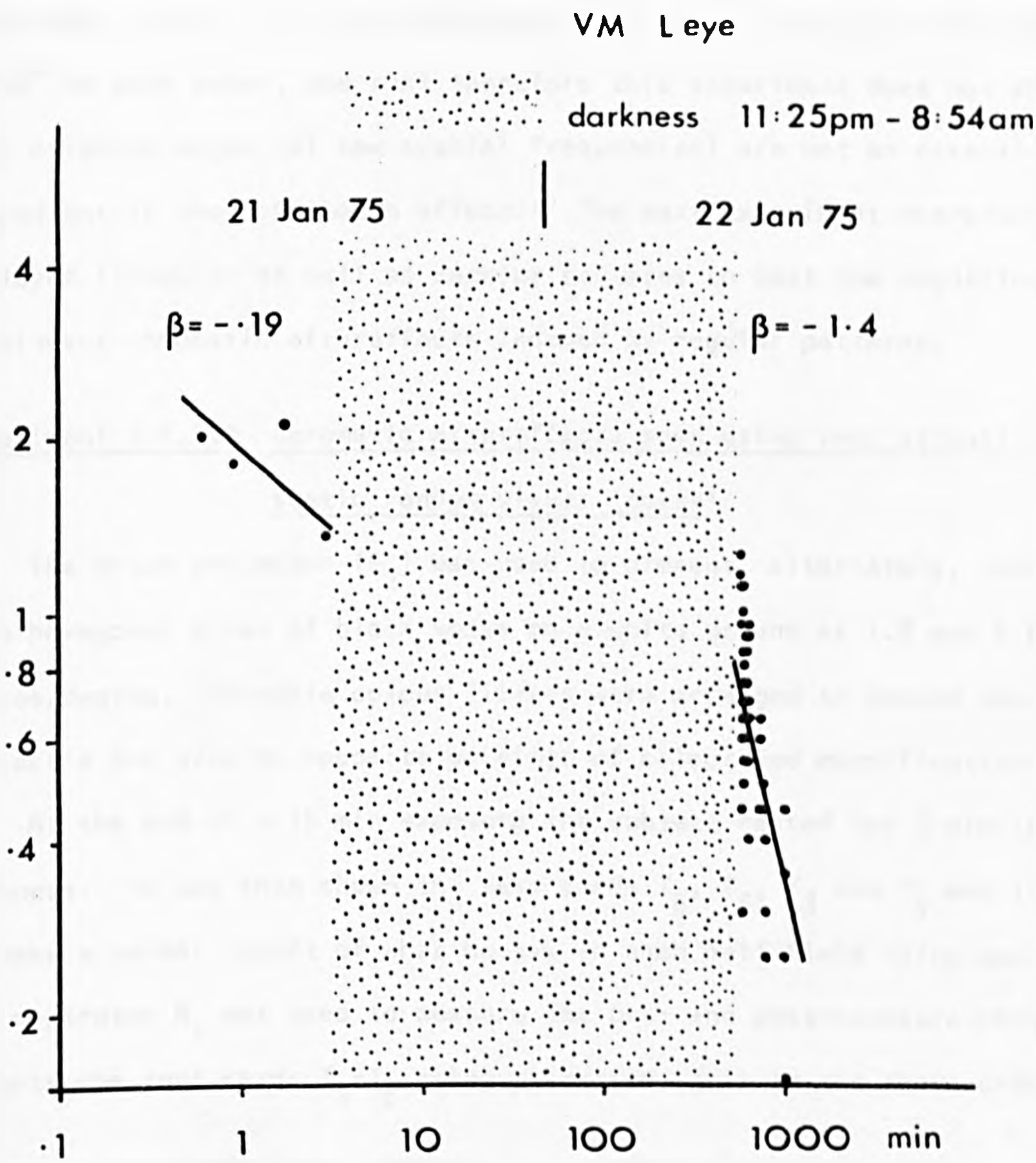


Figure 31 Retention overnight of the chromatic aftereffect contingent upon pattern spacing.

Discussion: It might be argued that the rows of spots used in the above experiment serve in fact as defocussed gratings at three orientations at 60° to each other, and that therefore this experiment does not show that oriented edges (of low spatial frequencies) are not an essential ingredient in the McCollough effect.* The next experiment therefore employed irregular as well as regular patterns to test the magnification-contingent chromatic aftereffects induced by regular patterns.

Experiment 7.1.1.2 Chromatic aftereffects seen using test stimuli of static random visual 'noise'

The Braun projector (E_2) was used to present, alternately, two slides of a hexagonal array of black spots on a white ground at 1.8 and 4.6 cycles/degree. Moveable colour filters were arranged to expose the subject's two eyes to opposite pairings of colour and magnification.

At the end of a 15 min exposure the subject rested for 2 min in darkness. He was then shown the test cards T_6, T_5, T_3 and T_4 and invited to make a verbal report of what he saw in each half field using each eye. The apparatus M_1 was used to measure the pre- and post-exposure chromatic effects, the test cards T_3-T_6 being presented again in the above order.

Results: Table 19 shows, for three subjects, the verbal and the measured pattern-contingent chromatic aftereffects. Positive readings indicate that the negative aftereffects were appropriate to the exposure stimuli.

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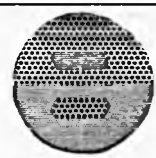
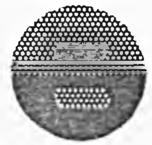
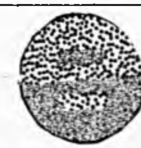
* The aftereffects induced by gratings when the projector was fully defocussed were only 1/3 less strong than when it was sharply focussed in spite of the fact that contrast was reduced by a factor of five.

Table 19

PCCA's seen on test figure: measured and verbal

S	Exposure Hexagonal array of black dots Duration (min)	Stimulus pairing		T_3 Regular black dots 				T_2 Regular white dots 				T_4 Random black dots 				T_5 Visual 'noise' 			
		L	R		L		R		L		R		L		R		L		R
VM	20	green large red small	red large green small	1.7	strong pink large clear green small	1.4	clear green large strong pink small	1.45	medium pink large clear green small	0.91	green large medium pink small	0.82	pale pink large clear green small	0.65	clear green large medium pink small	0.55	pale pink coarse clear green fine	0.32	clear green coarse distinct pink fine
MF	20	red large green small	green large red small	0	definite green large definite pink small	1.7	definite pink large definite green small	0	definitely green large slightly pink small	2.2	definitely pink large definitely green	-0.3	none possibly green small	0.8	definitely pink definitely green	0.3	none possibly green fine	1.1	definitely pink coarse definitely green fine
MAHM	20	red large green small	green large red small	1.2	definitely green large definitely pink small	0.4	definitely pink large definitely green small	1.1	definitely green large definitely pink small	0.9	definitely pink large definitely green small	0.52	green large pink small	0.27	pinker on large very vaguely green	0.55	green coarse pink fine	0.20	green coarse yellower - I think it must be greer

Comments: Since, in experiment 6.3.1 MF acquired a much weaker McCollough effect in his left eye than in his right, I attribute the weakness of effects in his left eye in this experiment also to the subject's eye and not to the stimulus condition. The effects in his right eye were very definite,and particularly significant since such small pre-test bias as he had evinced had been towards seeing the finer patterns as pinker than the coarser ones. Many subjects show such a (pre-exposure) bias, MAHM and VM included, and if this tendency operates also after exposure it is probably responsible for the slight assymetry in verbal and measured reports as between the right and left eyes of MAHM and VM. VM was struck by the definiteness of the green aftereffects she saw on both fine and coarse random patterns. Whereas generally after McCollough exposures she finds the pink aftereffect more remarkable than the green, in this case the green was quite as noticeable.

Findings: The spacing-contingent chromatic aftereffect is visible on randomly patterned test figures. It is at least a third as strong as on the regularly arranged patterns which match the inducing stimuli. The after-effect is reduced by a small amount (less than a third) when polarity of contrast in the test stimulus is the reverse of that used during induction.

Conclusion: Straight oriented edges are not essential for the detection of a McCollough-type spacing-contingent effect. The spacing contingent effect is sensitive to inversion of the polarity of contrast of the pattern.

7.1.1.3 Discussion: Polarity of contrast as a variable

On a Fourier analysis view (see 1.8) the latter finding is surprising since the spatial frequencies present in a pattern and its negative are identical. As a further test of the Fourier approach, it may be mentioned here that a purely 'phase' or polarity contingent chromatic aftereffect can be induced (of magnitude 1/6 that of the McCollough effect) using red and green inducing patterns which are photographic negatives of each other. Testing was performed on test figures like T_7, of 3.1 cycles/degree.

Such results demand a radical modification of the Fourier approach to include the dark/light dimension.

Experiment 7.1.1.4 Random patterns at two magnifications as inducing stimuli

Exposure for 30 min to random noise and to patterns of random dots, presented in red and green at two magnifications, produced significant but weak aftereffects which were seen on the corresponding random test figures by only a minority of subjects. Presumably the range of spacings present in the coarse and fine inducing stimuli overlapped considerably when the difference in magnification was only 2 (or 4 for the noise).

7.1.1.5 Summary: Spacing-contingent chromatic aftereffects.

Regular arrays of red and green spots at magnifications differing by a factor of two induce pattern-contingent aftereffects of over half the strength induced in the same time by McCollough grating stimuli. These aftereffects are visible on test figures which have average textures similar to those of the two inducing patterns yet are devoid of systematic orientation. The chromatic effects are reduced by reversal of the polarity of contrast of the test figure.

Like the McCollough effect these pattern contingent aftereffects follow power laws of decay and growth with exponents of about -1/3 and +2/3 respectively. They show no appreciable decay during a night's sleep.*

7.1.1.6 Is there an edge-sensitive ingredient in the McCollough effect?

The magnitude of the purely magnification-contingent effect - as compared with that of the McCollough effect induced in the same time by orthogonal red and green gratings - shows that spacing must be, at the very least, an important ingredient in the McCollough effect. The fact that the temporal properties of the spacing-contingent chromatic effect and of the McCollough effect are so similar suggests that a single mechanism mediates both. Or, if there are separate spacing and orientation sensitive mechanisms, they appear to possess very similar temporal properties. Indeed this similarity even raises the question whether orientational selectivity is a separate aspect of the McCollough effect or only a by-product** of a sensitivity to spacing which is separately modifiable in different directions at any point on the retina.

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* They can also be induced dichoptically (see chapter 6.1.1).
** See chapter 9.3.

7.2 A single oriented contrast edge

Whatever the mechanism, the McCollough effect undoubtedly has an edge and orientation sensitive ingredient: the chromatic aftereffects induced by a 20 min exposure to two coloured gratings can be clearly seen by most subjects on a test field consisting of a single black/white border. The pink or pale green colouration extends for about 1^o on either side of the edge. Considerably stronger effects are seen in the region of black or white thread on a contrasting background.

The strength of the above spacing-contingent chromatic aftereffect raises the question as to whether there is a cooperative response to texture in the McCollough effect. Is the effect induced by a grating larger than the sum of the effects induced by the individual edges it contains?

Experiment 7.2.1 A single edge as inducing stimulus

The apparatus M_1 was used to measure pre- and post-exposure pattern-contingent chromatic aftereffects, with test figure T_2 at 65 cm.

The inducing stimuli were semicircles of red and green on a black background (figure 32) projected sequentially by the Boots projector (E_3).

fig 32

on a screen at 3 m from the subject. The luminance of the red and green areas was 7 cd/m^2. To avoid inducing confusing ordinary chromatic aftereffects a set of four slides were used.

In a second experiment two 3/4° broad stripes of red and green were used as the inducing stimuli.

During the 20-30 min exposure the eyes were run to and fro across the edges through about 7° so as to expose the part of the retina to be tested to the stimuli.

Results: After both exposures, orientation contingent chromatic aftereffects were clearly visible on the test card T_2. Their decay is plotted in figure 33

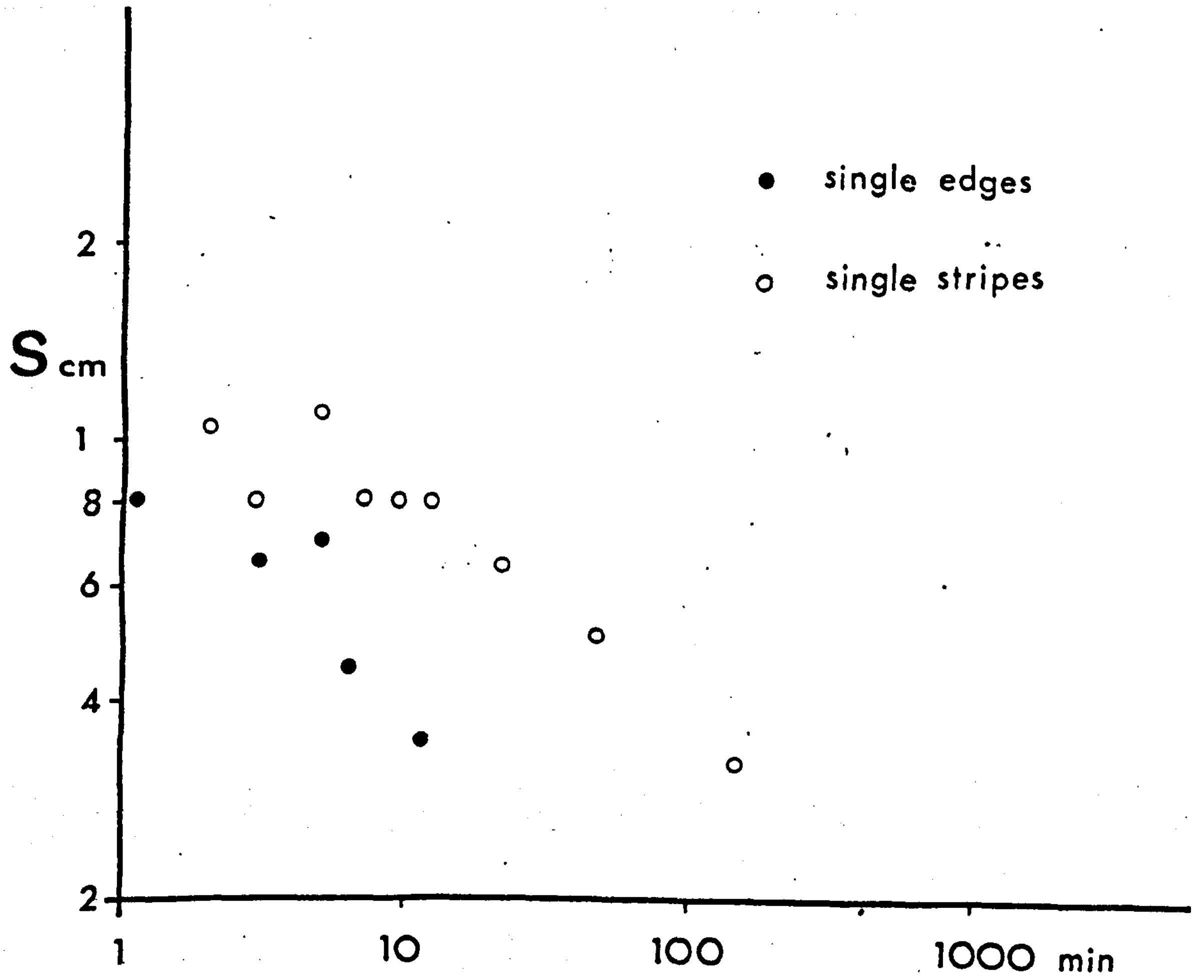
Findings: The aftereffect induced by the double-edged stripe was about twice as large as that induced by the single edge and they were comparable respectively with the effects produced in 2 min, 40 sec respectively (in the same subject at about the same date) by exposures to gratings of 2.2 cycles/degree which matched the test card T_2. Since in exposure to a grating (of 2.2 cycles/degree) each part of the retina exposed will be stimulated by an edge on average about 15, 30 times more, these ratios suggest very roughly that the effect induced by a grating is the sum of the effects induced by the individual edges.

Conclusion: A single edge and a single stripe can induce a McCollough effect. There is no strong indication that the effect induced by a grating involves lateral cooperative activity in addition to the effects induced by the individual edges.

Figure 33

Decay of the orientation contingent chromatic aftereffects seen on test figure T_2 (figure 2) after exposure to

- ● single edges (figure 32) for 30 minutes.
- o single stripes for 20 minutes.



7.3 Kinetic contours

In all the experiments on pattern contingent aftereffects so far described, the borders of the pattern elements have been defined by a luminance step. Since the visual system is also well equipped to detect edges defined by relative motion of textured fields, the question arises whether pattern contingent chromatic aftereffects might be inducible using such kinetic contours.*

Experiment 7.3.1 To find whether a McCollough aftereffect is visible on a test field of kinetic contours

The test field: Two identical black and white photographic prints of visual noise were used to produce stripes (3 cycles/degree) of pattern in relative motion. One set of stripes remained stationary while the others were agitated at about 5 Hz through $1/3^{\circ}$ longitudinally. A front silvered mirror was so held against this stimulus as to produce a view of two sets of juxtaposed stripes running at 90° to each other.

A large McCollough effect was binocularly induced by a 30 min exposure using apparatus E_1, but no chromatic aftereffect was visible on the above test field.

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* This was my husband's suggestion.

Experiment 7.3.2 To find whether a McCollough type aftereffect can be induced using kinetic contours

The agitated stripes of visual noise just described were used as the inducing stimulus. They were (binocularly) viewed alternately by red and by green light when tilted at +45° and -45° to the vertical for 10 sec apiece with a 3 sec dark period for a total of 20 min. Subsequent (binocular) testing was performed on the kinetic contours as in the preceding experiment and on the test figure T_2, but no chromatic aftereffects were seen.

Conclusion: Though kinetic contours can form a very clearly visible grating pattern they are not a stimulus which can induce an orientation-contingent chromatic effect nor render visible an existing McCollough effect.

A real difference in the intensities at the receptors appears to be necessary in McCollough stimuli.

7.4 Simultaneous contrast* colours

An attempt to induce a McCollough effect by means of achromatic gratings encircled by red and green fields produced no detectable chromatic aftereffect. It must, however, be added that control experiments in which delicate tinting was added (by means of one layer each of cinemoid

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* I am indebted to Professor D. Hubel for the idea for this experiment. He remarked that he would find it difficult to believe that the site of the McCollough effect was not cortical if an effect could be induced using Land colours.

38 and 54) to the gratings yielded barely perceptible aftereffects.

It is possible that real difference in the group of receptors stimulated is an essential ingredient of the stimulus for inducing a McCollough effect.

7.5 Contours visible by virtue of persistence of vision

Moderate aftereffects (S approximately equal to 0.5 cm) were induced by 15 min spent viewing alternately a row of red and a row of green dots each of which moved at about 19°/sec in a direction perpendicular to itself. The hues of the aftereffect seen on test figure T_2 were appropriate to the orientations of the perceived 'stripes' and not to the orientation of the two lines of dots.

7.6 Summary: Essential features of McCollough stimuli

Red and green patterns which differ in magnification are effective stimuli for inducing large and long-lasting pattern-contingent chromatic aftereffects. The aftereffects are visible upon random stimuli which differ only in the average size of the pattern elements. In their time constants of decay and growth, and in being retained in darkness, these aftereffects closely resemble the McCollough effect.

A McCollough effect can be induced by a single edge between a black and a coloured field. There is no strong indication that a grating induces an effect which is more than the sum of the effects produced by its single edges.

The stimuli for inducing and for testing McCollough aftereffects must contain contours defined by a step in luminance at the primary receptors. Kinetic contours are ineffective as McCollough stimuli.

Chapter 8 The Angular Distribution Function of the McCollough Aftereffect

8.1 Investigation of the opponent colour 'orthogonal inhibition'

Hajos (1970, 1973) had claimed, for reasons explained in chapter 2.4.7, that the McCollough aftereffect had an opponent-colour component at the orientation orthogonal to the inducing grating. This interesting complexity, either of the McCollough mechanism itself, or of the mechanisms feeding it, seemed worth investigating. There were three circumstances in which we expected to find signs of it:

a) When two orthogonal McCollough exposure gratings have the same (instead of complementary) colours there should be signs of mutual cancellation of their aftereffects. For example,* the chromatic aftereffects produced by exposure to a succession of four gratings at 45° to each other in alternating colours should be smaller than that produced by six similar gratings at 30° to each other.

b) When three exposure gratings of alternating colours make small angles with each other there should be a ripple of zero crossings at the orientation orthogonal to the gratings.

c) After exposure to a single coloured grating, the aftereffect of the same hue should be visible upon an orthogonal achromatic grating, particularly if a white comparison field is provided.

Experiment 8.1.1 Multiple orientation-contingent chromatic aftereffects (OCCAs)

The inducing stimuli were presented by the Boots autofocus projector E_3 and subtended 19° x 20° at a range of 103 cm. The stimuli were

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* This experiment (8.1.1), was suggested by my husband and started our interest in this aspect of the McCollough effect.

red/black or green/black gratings subtending 2.2 cycles/degree, luminance 17 mlm and 2 log units contrast. The sets of gratings used in different runs had orientations separated from each other by 90°, 45°, 30°, 22½° and 15° around the clock and were of regularly alternating colours. The various orientations were presented repeatedly in clockwise and then in anticlockwise order (alternately red and green slides), for 7 sec apiece with a 1 sec dark period. Each of the inducing gratings was exposed for a total time of 10 min (including dark intervals), so that the overall induction times for the sets of gratings with the separations mentioned were 20, 40, 60, 80 and 60 min respectively. (For the 15° run, only 7 of the 12 possible orientations were presented. Those at -45° and +45° were exposed for only 5 min each so as to equalize the total time spent in red and in green light.) Every exposure period was followed by a 10 min rest in darkness.

The pre- and post-exposure measurements were made using apparatus M_2 with test figure T_1 at 65 cm (gratings 2.0 cycles/degree) illuminated at 0.45 mlm. The Dove prism was stepped sequentially clockwise and back, the subject making one hue match of the annulus to the achromatic grating at each position on each traverse. Including a short halfway rest for the subject, each set of readings took about 7 min.

<u>Results</u>: Figure 34a shows in polar form the OCCAs for separations of 90°, 45°, 30°, and 22½°; the two traverses each begin at the top right-hand corner. To make possible quantitative comparisons the experiment was repeated (figure 34b) with matched testing conditions (in which roughly the same number of readings were made in a traverse for each run). Figure 34b is plotted on Cartesian coordinates with orientations anti-clockwise from horizontal positive. For figure 34b the results for the

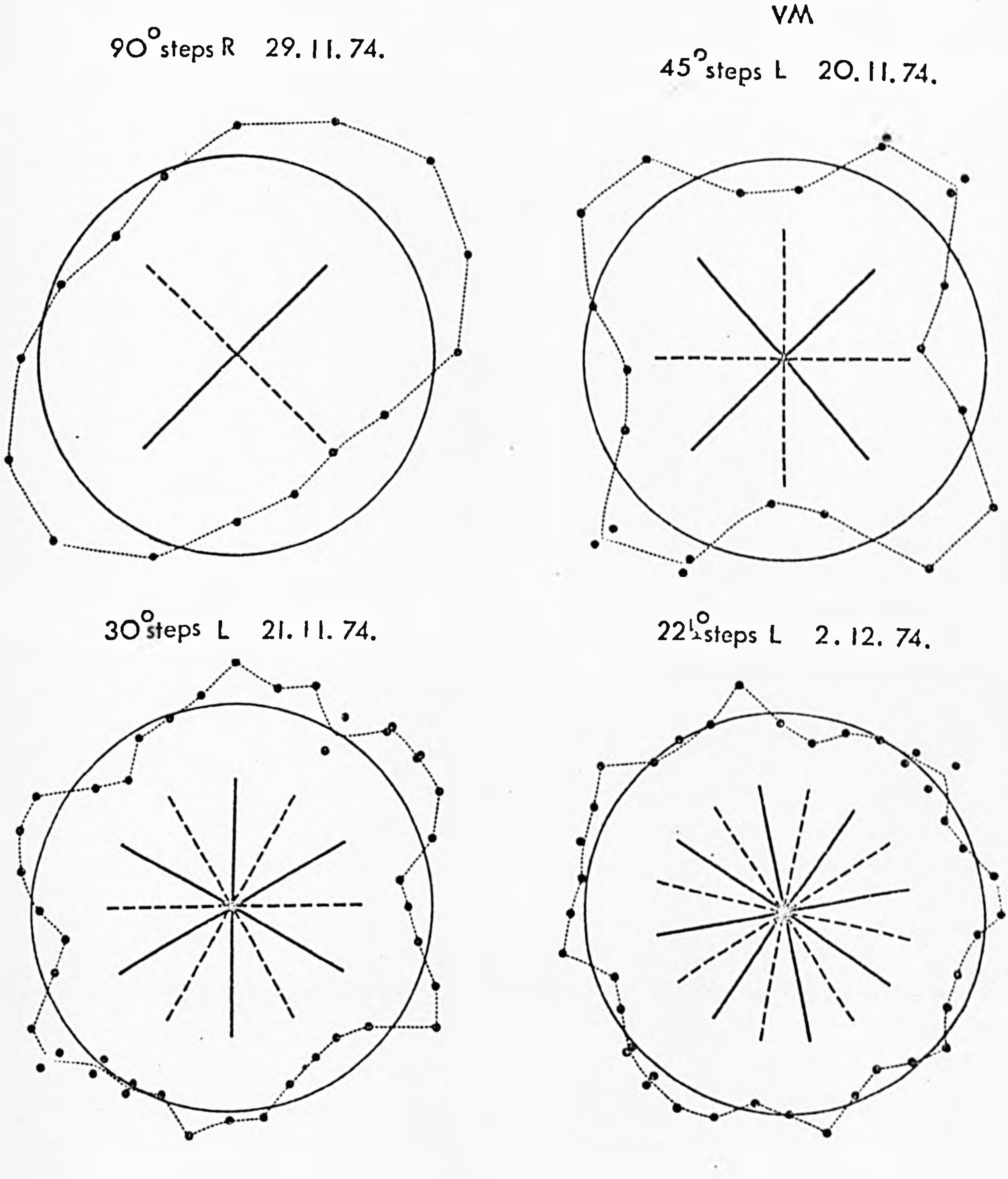
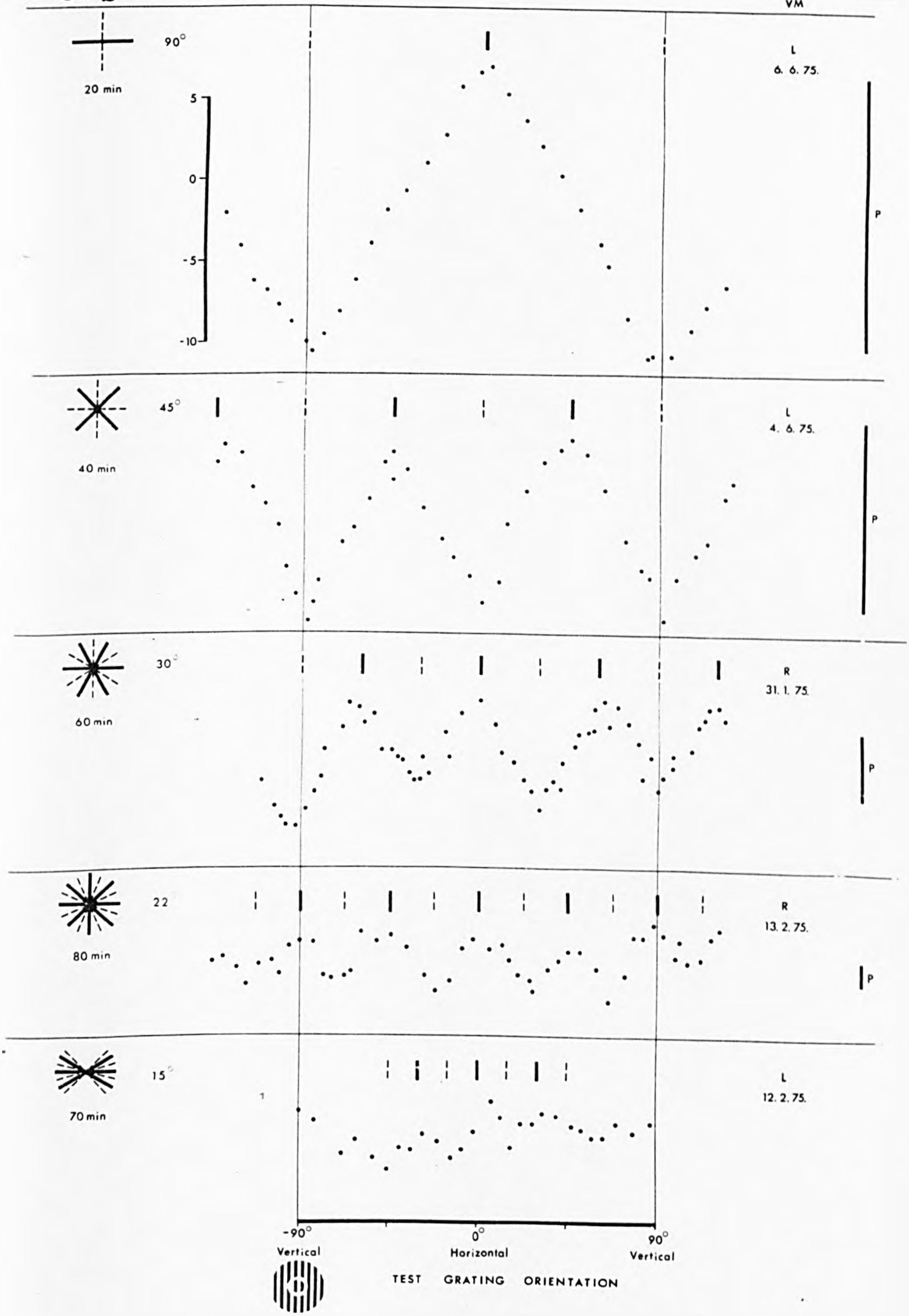


Figure 34 Experiment 8.1.1

a) Polar plots of angular distributions of OCCA for multiple red and green gratings with orientations (as shown) separated by steps of 90°, 45°, 30° and 22½°.

b) Cartesian plots for similar runs (with separations down to 15°) to test predictions of magnitudes. Bars marked P at right show peak to peak magnitudes predicted by summing distributions for each grating separately.

Green aftereffects are plotted in a) radially outwards, in b) upwards.


VM
20 min
90°
L
6. 6. 75.
5
0
-5
-10
P
45°
40 min
L
4. 6. 75.
P
30°
60 min
R
31. 1. 75.
P
22
80 min
R
13. 2. 75.
P
15°
70 min
L
12. 2. 75.
-90°
Vertical
0°
Horizontal
90°
Vertical
TEST GRATING ORIENTATION

clockwise and anticlockwise traverse are averaged in all except the 30° run. Throughout figure 34b the results are corrected for the small average biasses revealed by the pretest.

The length of the vertical bars at the right of figure 34b (marked P) indicates the peak to peak amplitudes of the distribution functions predicted, as will be described in 8.2.2, by simple summation of the aftereffects of the individual gratings.

In all but the 15° case the alternations of hue were clearly visible on a 'ray' test figure (MacKay, 1957), having 1.7° black and white sectors.

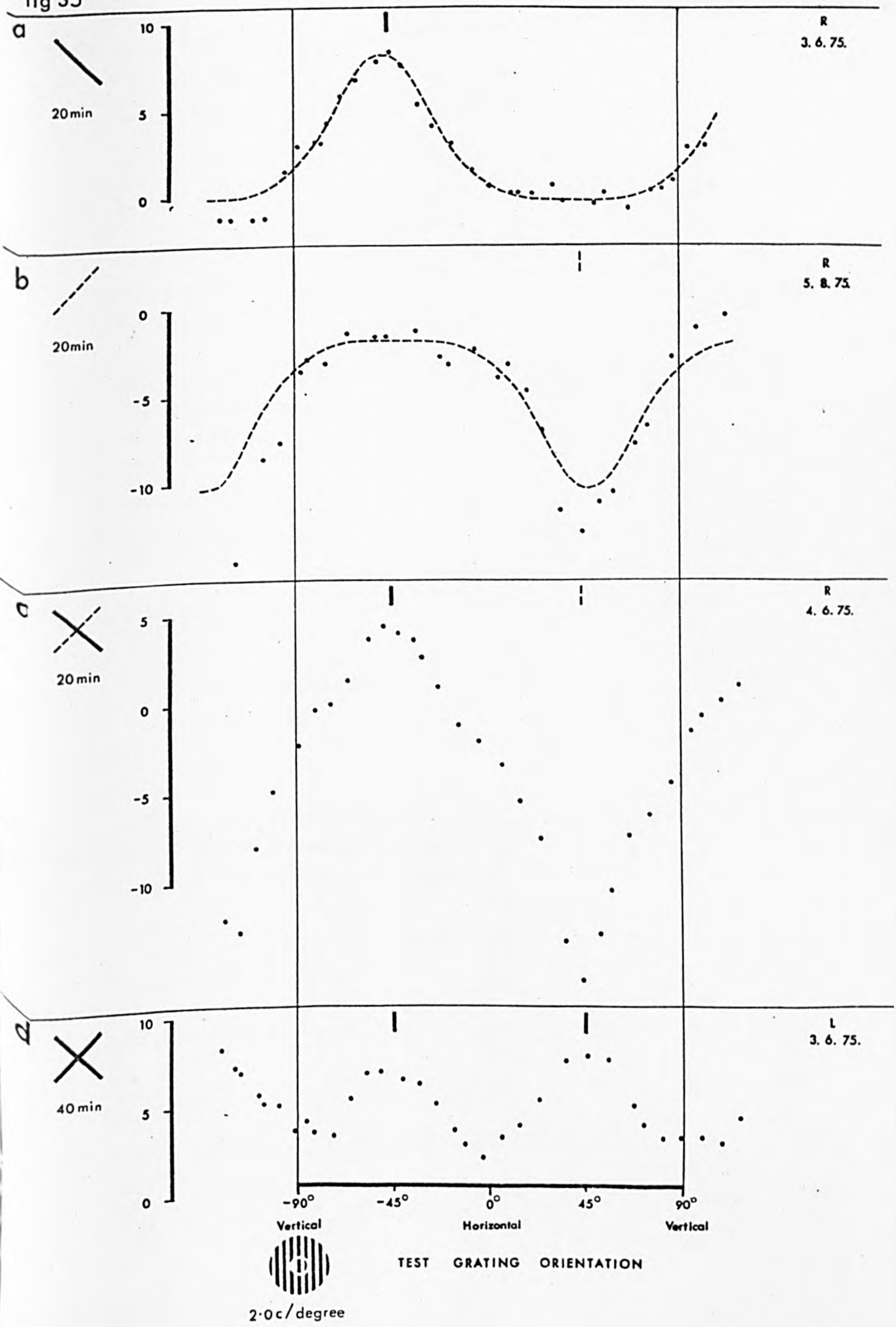
<u>Findings</u>: Thepeak to peak strengths of the OCCAs decreased progressively as the gratings were placed at smaller angles to each other. There were no signs of a periodic variation in aftereffect strength as inducing gratings of the same or complementary colours were set perpendicular to each other.

This absence of the anticipated signs of mutual cancellation of the aftereffects sent me back to Hajos's (1970, 1973) experiments and the controls (see 2.4.7) which seemed desirable, and also the experiment with two red gratings at right angles which needed to be performed to clarify what does occur in 'neutralisation'. Across these runs I kept the subject's state of chromatic adaption as similar as possible by alternate exposure to red and green fields in an identical time sequence.

Experiment 8.1.2 The OCCAs produced by one grating and by two orthogonal gratings of the same and of differing colours

The apparatus and methods were as in experiment 8.1.1. In addition to grating stimuli at $\pm 45^{\circ}$ to the vertical, plain coloured fields of the same average luminance (8.5 mlm) and extent were also presented.

fig 35


VM
a
20min
10
5
0
R
3. 6. 75.
b
20min
0
-5
-10
R
5. 8. 75.
c
20 min
5
0
-5
-10
R
4. 6. 75.
d
40 min
10
5
0
L
3. 6. 75.
-90°
Vertical
-45°
0°
Horizontal
45°
90°
Vertical
TEST GRATING ORIENTATION
2·0 c/degree

Results: Figure 35 shows angular distributions of OCCA following a total of 20 min of exposure (including dark periods) in each case to:
a) a single red grating at -45° alternating with a plain green field;
b) a single green grating at +45° alternating with a plain red field;
c) an alternating sequence of the gratings of a) and b), as for the normal McCollough exposure.

For comparison, Figure 35d shows results for a run where the inducing gratings, viewed for a total of 40 min, were both red, at -45° and +45° respectively, interleaved with plain green fields as in a).

Runs in which the unpatterned coloured fields of a) and b) were replaced by totally dark fields gave results similar in form, but with the magnitude decreased by more than a third.

Findings and Conclusions: The aftereffects produced by exposure to a red and to a green grating have similar, bell shaped angular distributions of half width approximately 26°. In the region, extending over about 40-50°, at right angles to the inducing grating the curve was nearly flat

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Figure 35 Experiment 8.1.2

Angular distributions of OCCA following exposures to:

a) a single red grating at -45° alternated with a plain green field of the same average luminance for a total time of 20 min.

b) a single green grating at +45° alternated with a plain red field. Total 20 min.

c) a normal McCollough sequence of the gratings of runs a) and b). Total 20 min.

d) a repeated sequence of a red grating at -45°, unpatterned green field, red grating at +45° and unpatterned green field. Total 40 min.

Orientations of inducing gratings are shown to left of corresponding graph.

Dotted curves show the smoothed symmetrical approximation used in later predictions (see text).

and there was no clearly perceptible hue. As judged relative to the level of the pretest (indicated by zero on the scale at left) the hue in this region did not cross to the complementary colour. On paper test cards like T_9, T_{10} having a white comparison area, no consistent hue difference was detectable at these angles. On T_8, however, which has a grating parallel to the inducing grating, the parts of the test card took on complementary hues (as observed by Stromeyer, 1969), presumably because of simultaneous contrast.

The dotted curves are the average of smooth lines through the results of runs a) and b). These curves are very close to a Gaussian with points of inflexion at $\sigma = 22\frac{1}{2}^{\circ}$. They are used later as the basis for predictions (8.2.2).

The distribution of readings for c) is reasonably close to the sum of the dotted curves in a) and b). From the reduction of the after-effect when the unpatterned fields were omitted, we concluded (MacKay and MacKay, 1977b) that "interleaving with a differently coloured stimulus selectively favours the chromatic mechanisms that respond to the coloured grating, in the manner exploited in Stiles's two colour threshold method (1949)". When the unpatterned red field was omitted from run b) its peak to peak difference became only a third of that in c). It was just such a difference, produced using such stimuli, that Hajos ascribed to the 'heterochrome orthogonal inhibition'.

In run d), the measured distribution is again about the sum of those for single red gratings at the same orientations, giving twice as many maxima as the normal effect c). (Hajos, 1970, makes the same observation with regard to the OCCA, which he produced using two green orthogonal gratings, with no interleaved red fields.) In MacKay and

MacKay (1977b) we suggested that this run reveals how 'neutralisation' can appear to occur if one uses a test field of two orthogonal gratings, (Stromeyer, 1969, 1972) instead of one with a white comparison field:

"Build up of the effect of the second inducing grating would be expected to abolish the observable contrast in hue between the test gratings without necessarily cancelling the physiological aftereffect of the first."

The above control experiments show that none of the evidence from 1969 to 1972 which had been taken to indicate a 'heterochrome and orthogonal inhibition', compelled such a conclusion.

Experiment 8.1.3 Three gratings at small angular separations

The apparatus and method were as for experiment 8.1.1. Figure 36 shows distributions obtained after 35 min exposure to alternating red and green gratings at angles of $22\frac{1}{2}^{\circ}$ to each other. (Five minutes of exposure to unpatterned red fields was included to roughly equalise the times spend viewing each colour.)

Findings: There is no significant 'ripple' towards a red aftereffect at -45°, the direction perpendicular to the red inducing grating.

It was now clear that to determine whether there was an orthogonal effect at all, a sensitive means of comparing a very pale aftereffect with a white comparison field was called for. Apparatus M_3 allows measurement by either hue-comparison or hue-cancellation, the comparison in each case being between a single rotatable grating and an unpatterned area (see 4.2.1).

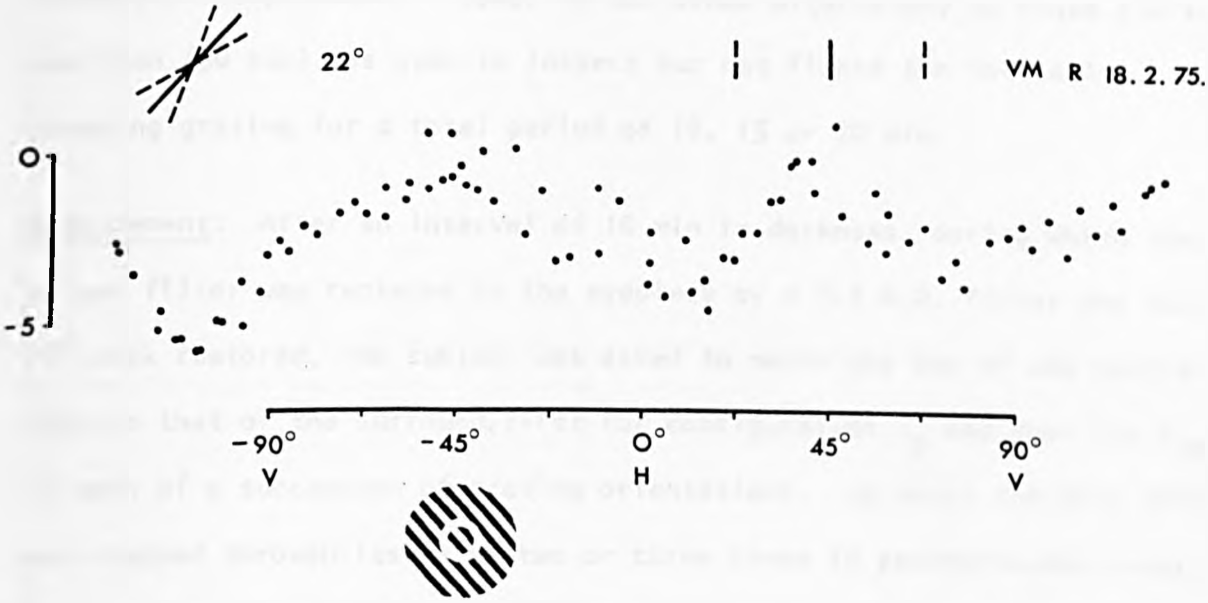


Figure 36 Experiment 8.1.3

The angular distribution of the OCCAs of exposure to a red and two green gratings at angular separations of $22\frac{1}{2}^{o}$.

Experiment 8.1.4 Angular distribution of the OCCA for a single inducing grating

Inducing exposure: To facilitate comparisons between the orientations of gratings used in exposure and testing, in this experiment the test apparatus (M_3) was also used to present the inducing stimuli. Identical slides of vertical gratings (or, for the control runs, unpatterned slides) were projected simultaneously by P_1 and P_2, and the 15^o circular mask defining the outer edge of the test field was removed to give a larger field ($19^o \times 20^o$ at 56 cm). During exposure a colour filter was attached to the eyepiece, either red: Cinemoid 14 'ruby', 590-670 nm (1 layer); or green: Cinemoid 24 'dark green' 480-560 nm (2 layers). This gave a luminance of 1.9 mlm in light areas and contrast 1 log unit.

The subject (Ishihara normal) sat in a darkened room using a bite bar, and wearing a black patch over the non-viewing eye. As in Stromeyer's experiment 2 (1969) he was asked alternately to close (10 sec) and open (50 sec) his eyes to inspect but not fixate the vertical inducing grating for a total period of 10, 15 or 20 min.

Measurement: After an interval of 10 min in darkness, during which the colour filter was replaced on the eyepiece by a 0.3 N.D. filter and the 15^o mask restored, the subject was asked to match the hue of the central area to that of the surround, first for configuration T_9 and then for T_{10}, at each of a succession of grating orientations. In total the Dove prism was stepped through its range two or three times in pseudo-random order. The subject closed his eyes while the prism and slides were changing, i.e. for a total of 6 min of the 15 min spent on one set of readings. The difference between the matching settings for T_9 and T_{10} at a given angle was taken as a measure of the OCCA and was plotted (green conventionally positive) against grating orientation. (Orientations anticlockwise from horizontal are plotted as positive.) A pretest run was routinely made in identical fashion for all orientations before each inducing exposure.

Results: Typical resulting angular distributions of the OCCA are shown in figure 37a. Only one half of the angular range was covered, in random order, so as to reduce systematic errors due to the decay of the OCCA with time. (Each point is the average of three measurements, and the zero-level is the average of all four sets of pretest readings.)

No significant reversal of OCCA polarity was found at right angles to the inducing orientation, nor was any verbally reported in answer to questions. If anything the readings there seemed to settle at a non-zero level of the same sign.

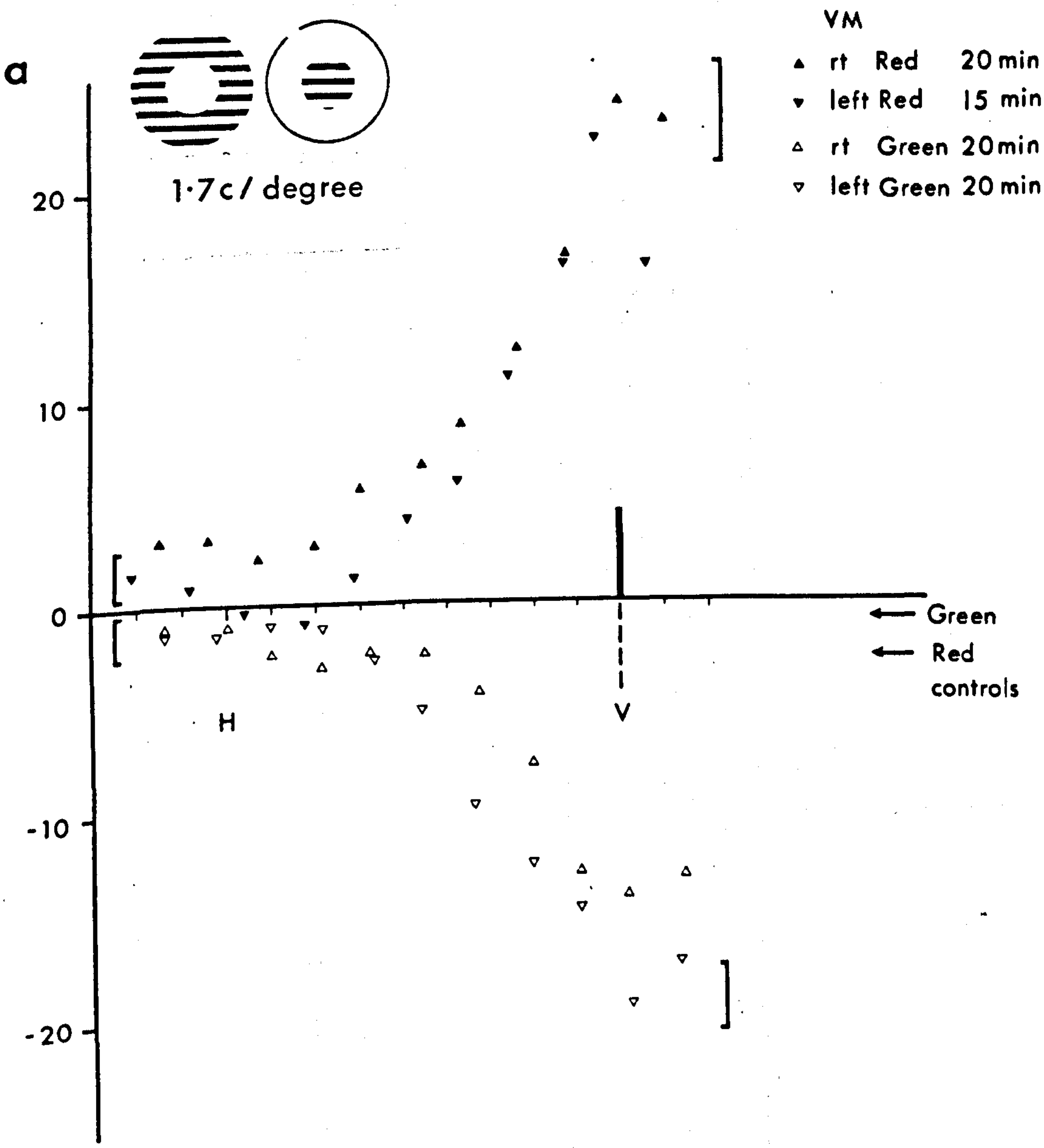
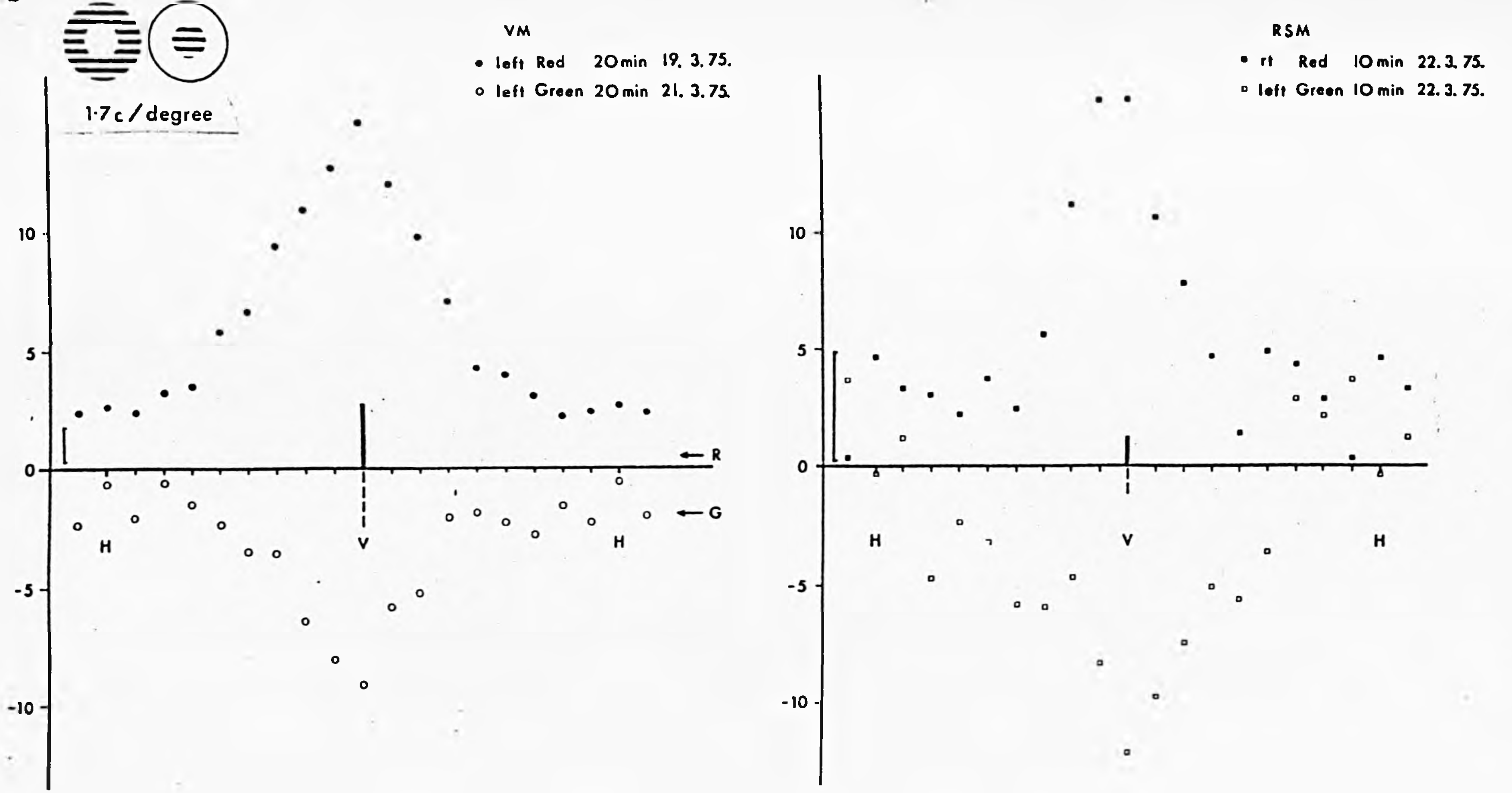


Figure 37 Experiment 8.1.4

Angular distribution of OCCA following exposure to a single vertical red or green grating of 1.7 cycles/degree (a and b) and 3.5 cycles/degree (c). ▲▼and △▽ denote exposures to red and green gratings respectively at the angle to the horizontal indicated on the abscissa. Longer bars indicate longer exposures. Note that the red and green exposures in each pair of experiments, though paired on the graph for comparison, took place on separate occasions.

The small inset discs represent (not to scale) the test figures used. The abscissa (10° divisions) shows the orientation of the test grating. The ordinate shows the strength of the aftereffect as the difference between matching settings for each pair of test configurations. This measures linearly the excess of red over green light (or vice-versa) required for a subjective match (see text). Error bars indicate twice estimated S.D., for points in the region of horizontal and vertical respectively. Horizontal arrows show the average overall test angles for control runs with unpatterned fields.

37b


1·7 c / degree
VM
● left Red 20 min 19. 3. 75.
○ left Green 20 min 21. 3. 75.
10
5
0
-5
-10
H
V
H
← R
← G
RSM
▪ rt Red 10 min 22. 3. 75.
▫ left Green 10 min 22. 3. 75.
10
5
0
-5
-10
H
V
H

37 c

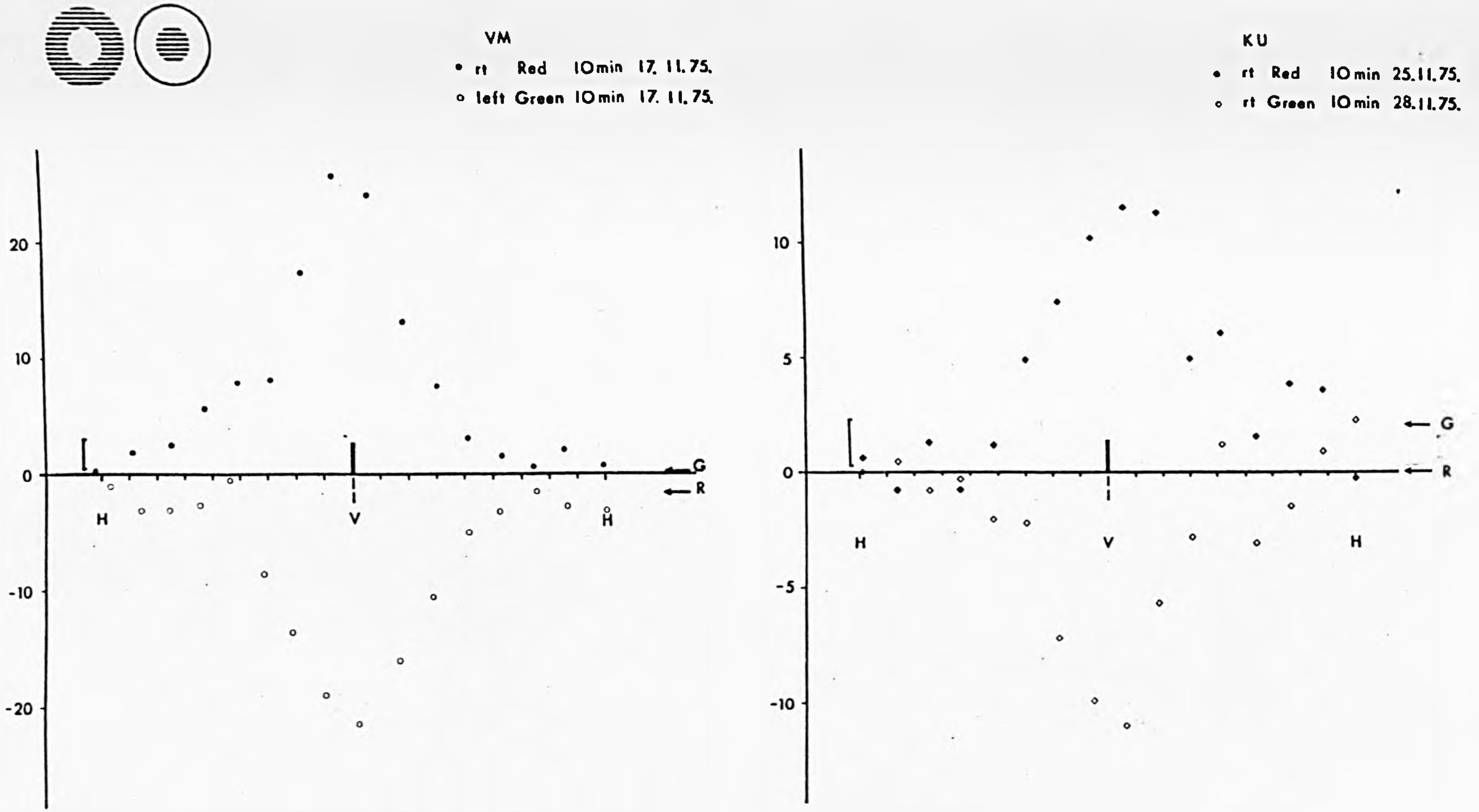

VM
• rt Red 10 min 17. 11. 75.
○ left Green 10 min 17. 11. 75.
20
10
0
-10
-20
H
V
H
G
R
KU
• rt Red 10 min 25.11.75.
○ rt Green 10 min 28.11.75.
10
5
0
-5
-10
H
V
H
G
R

Figure 37b shows two pairs of runs covering the whole angular range to investigate this point further.

In order to see whether the shape and width of the angular distribution function depended critically on grating frequency, the experiment was repeated using finer gratings (inducing and test) of 3.5 cycles/degree. The results, shown in figure 37c, are not significantly different.

8.1.5. A further experiment was performed in which exposure was to alternated red and green vertical gratings of 2.2 and 5.4 cycles/degree, and hue settings were made at all orientations using T_{11} and T_{12} alternately in apparatus M_3. The resulting curves were of similar form to those of figure 37 , and had a small residual bias at all angles. It seems likely therefore that the truth concerning the orthogonal effect after such an inducing exposure lies somewhere between the reports of Leppmann (1973) and Lovegrove and Over (1972). (See chapter 1.6.)

8.1.6 Summary: The angular distribution function of the OCCA produced by a single, coloured grating

These results seem to tell conclusively against the idea of chromatic opponent coupling between orthogonal orientations in the visual system. Induction of an OCCA by a grating in one orientation and colour neither produces a complementary OCCA at right angles, nor tends to neutralize the OCCA induced by a similar but orthogonal grating (though it does of course tend to reduce or abolish the contrast in hue between two orthogonal test gratings). As already found in similar experiments by Hajos (1970, 1973) and Keys, Hensley and Matteson (1971, unpublished), the distribution function is close to a Gaussian curve with a width (2σ) of about 45° between its points of inflection.* This sits on a small

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* I have not found any evidence of the subsidiary maxima-'zwischen maxima'-mentioned by Pieper (1976, p. 108).

residual bias of the same polarity at all orientations, which is presumably a pure contour-density-contingent effect similar to those described by Leppmann (1973) and MacKay and MacKay (1975a). Doubling the spatial frequency of the inducing and test gratings does not significantly affect the angular distribution.

These experiments left open the question raised in chapter 3.2.3.2 as to whether coloured gratings might - like achromatic line stimuli - produce interacting effects.

8.2 Summation of the effects produced by gratings at acute angles

Introductory: Angular resolution and angular interaction in the McCollough effect?

Interaction between the effects of lines at an angle to each other, whether presented simultaneously or sequentially, is so prominent a feature of perception that it seemed possible that the McCollough effect might have an angle sensitive aspect. (3.5.2)

Dr. J.J. Kulikowski expressed interest in our experiments with four and more gratings and encouraged me to determine the angular resolution of the McCollough system. This was done with a) increasing numbers of equally spaced gratings, when as we have seen (experiment 8.1.1) the limit of resolution was reached at about 15° separation, and b) with a pair of gratings of complementary colours. This was in a sense a repetition of Linda Fidell's (1970) investigation from which she concluded that 'aftereffects are not produced to patterns at the same orientations if the other adapting pattern is of less than 22°

divergence'. But, where she had tested the aftereffects on a pair of gratings only at the same orientations as the inducing gratings, I recorded the entire angular distribution of the OCCA.

Experiment 8.2.1 The resultant aftereffect produced by alternate exposure to a red and a green grating at an acute angle to each other

Apparatus and methods were as in experiment 8.1.1. A red and a green grating at angles to each other of 60°, 45°, 30°, 22½°, 15° and 11° were presented alternately for 7 sec apiece for a total of 20 min.

Results: Figure 38a shows the angular distribution of the OCCAs for some of these cases. In each case the dotted line, superimposed for comparison, represents the prediction generated by the simple summation of the curves for a red and for a green grating shown in figure 35a and b. Figure 38b shows, for several runs, the variation of the angle between the recorded maxima of the OCCAs, with the angular separation of the inducing gratings.

Subjects who were invited to turn the Dove prism themselves to the orientations at which the test field appeared most colourful, selected orientations which agreed with the positions of the maxima in the above graphs.

Findings: The magnitude of the OCCAs fell smoothly with decreasing angular separation of the inducing gratings until, at 11°, the aftereffects were barely visible.

The maxima of the aftereffects were found not at the orientations of the inducing gratings, but 'repelled' to greater angular separations. The repulsion, for small angles between the inducing gratings, is 20°-30°.

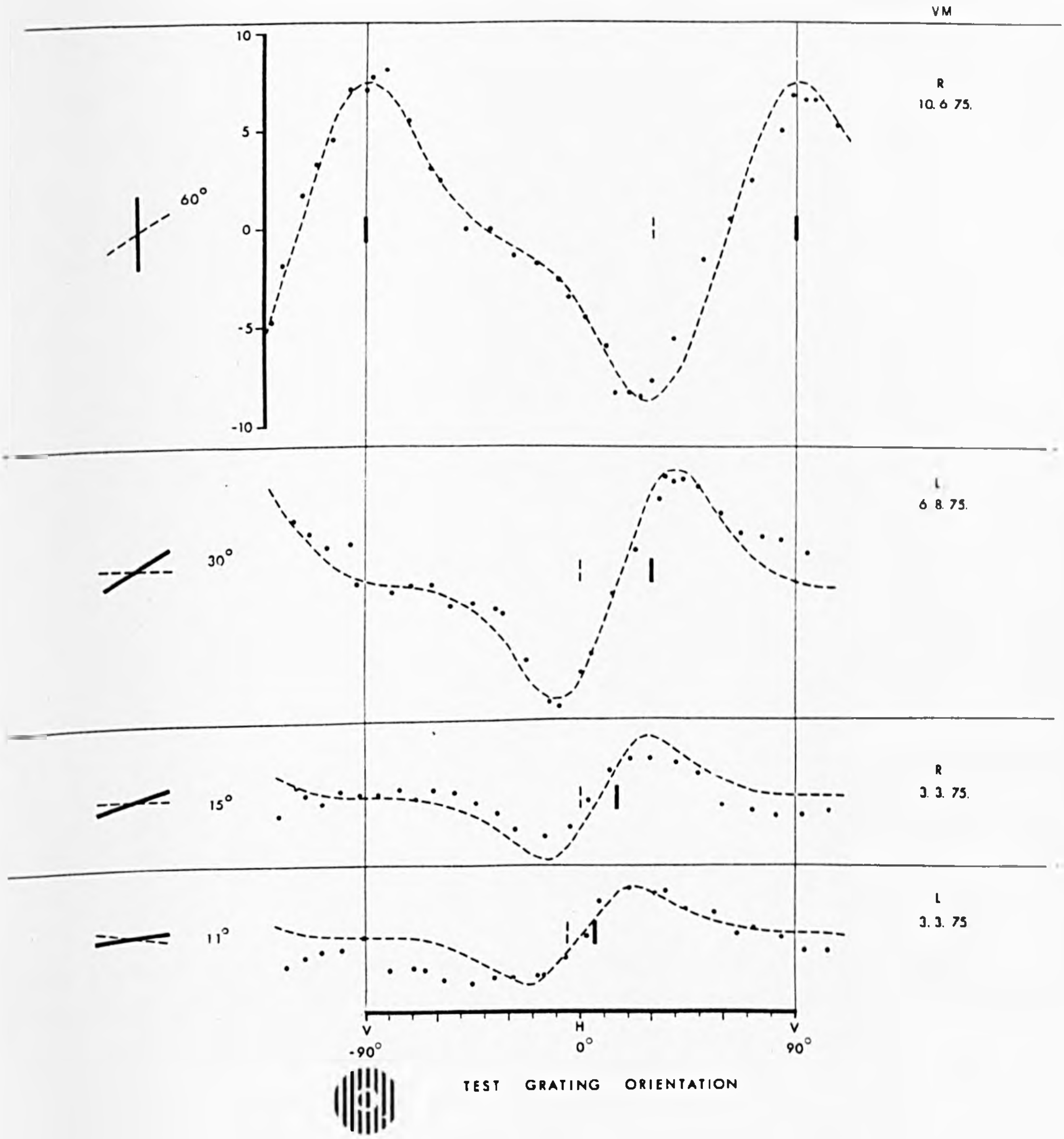

Figure 38 Experiment 8.2.1

a) Angular distributions of OCCA following 20 min exposures to pairs of gratings separated in orientation by 60°, 30°, 15° and 11°. The dotted curves represent simple summation of appropriate curves for single red and green gratings (Figure 35a and b).

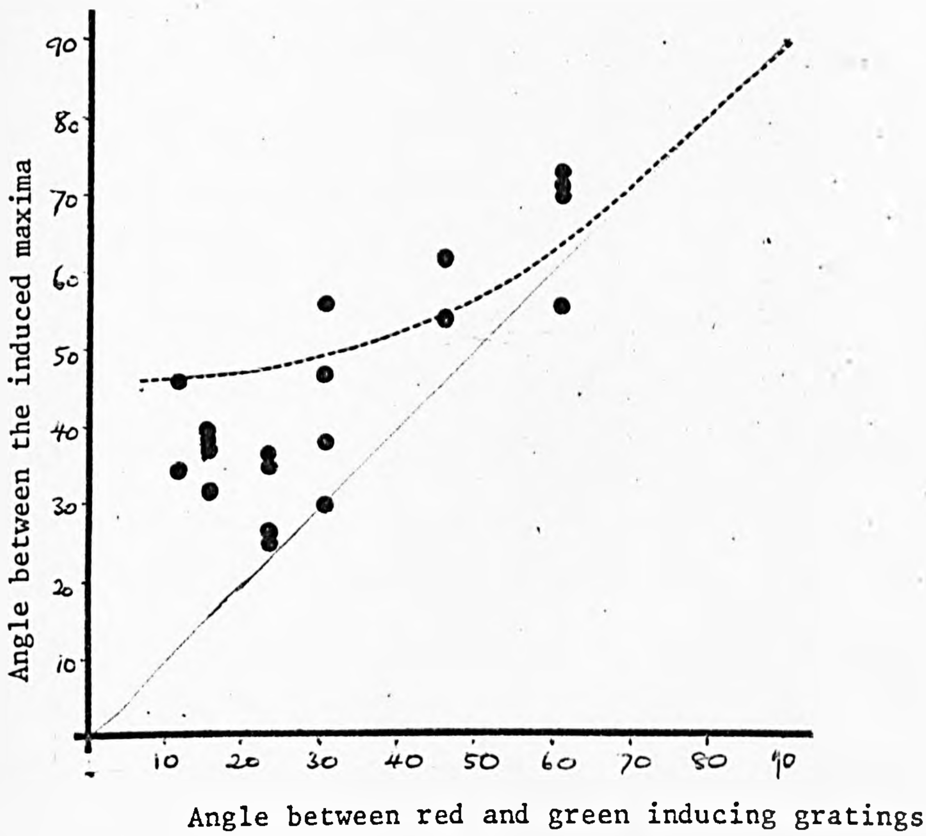

Figure 38 Experiment 8.2.1

b) The variation of the angle between the induced maxima with the angle between the inducing gratings, for runs like those of figure 38a. The dotted line shows the values predicted from the dotted curves of figure 35a and b for which $\sigma = 22\frac{1}{2}^{\circ}$.

8.2.2 Discussion: Simple summation with no lateral interaction

This 'repulsion of the maxima' might, at first sight, be taken to indicate that there is interaction between the effects produced by the two gratings (compare White and Riggs, 1974, quoted in 3.2.3.2). However, the apparent summation of the effects of a red and a green grating at right angles, which had been observed in experiment 8.1.2 (figure 35 a, b and c) suggested that a similar arithmetical approach might be applied to the aftereffects of gratings at smaller angles. Only if the prediction by simple summation left a residuum of features unaccounted for, need angular interaction be invoked.

The Gaussian curve derived by averaging the results for the red and for the green grating in figure 35a and b was used to make the predictions shown dotted in figure 38a and to calculate the peak to peak magnitudes in figure 34b. Although the scatter for the readings is considerable the general agreement of the shapes, and to a lesser extent, the magnitudes of the predicted and measured distributions is clear. In particular the predicted orientations at which the maxima occur correspond well with the observed 'repelled' positions. (The experimental results would probably have been better fitted in all respects by a slightly narrower Gaussian, with σ, the standard deviation, 21 or 22° in place of 22½$^{\circ}$.)

The 'repulsion'- greatest for small angles of divergence - is mathematically to be expected when any pair of roughly symmetrical curves each with a single maximum are simply subtracted. Their difference when they are slightly displaced approximates to their first derivative and has its maxima at the points of inflexion of the original curve.

Conclusion: The McCollough effects produced* by two or more red and green gratings at any** angles to each other are predictable in magnitude and angular distribution from simple summation of the aftereffects produced by each grating separately (complementary colours being assigned opposite signs). No additional mechanism such as lateral inhibitory action between orientation-specific channels need be postulated to account for the 'displacement' of the maxima.

If, as the above conclusion suggests, the McCollough aftereffects produced in a single eye by differently oriented coloured gratings are totally independent, they should have independent decay courses.

Experiment 8.2.3 The decay courses of aftereffects induced at different times and different orientations in the same eye

Two pairs of 30° divergent red and green inducing gratings were used, one pair oriented near vertical, the other near horizontal. The apparatus was as for experiment 8.1.1. The object was to see whether the time course of the aftereffect of one pair was noticeably affected by that of the other pair exposed an hour later, or whether the two were independent.

Results: Figure 39a shows a series of angular distributions measured in the course of the experiment. The first (i) is the pre-exposure

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* This assumes that the same state of chromatic adaptation of the eye is maintained in each run by suitable alternation of red and green stimuli.

** Several other combinations of orientations have been tried. The most interesting case was that where two green gratings were used at separations of 34 - 54°. The observed angular distributions agreed well with predictions. The two peaks, at the inducing orientations, which in the 54° case were separated by an 8% trough, became almost indistinguishable in the 45° case and totally indistinguishable in the 34° case, both subjectively and in the measurements.

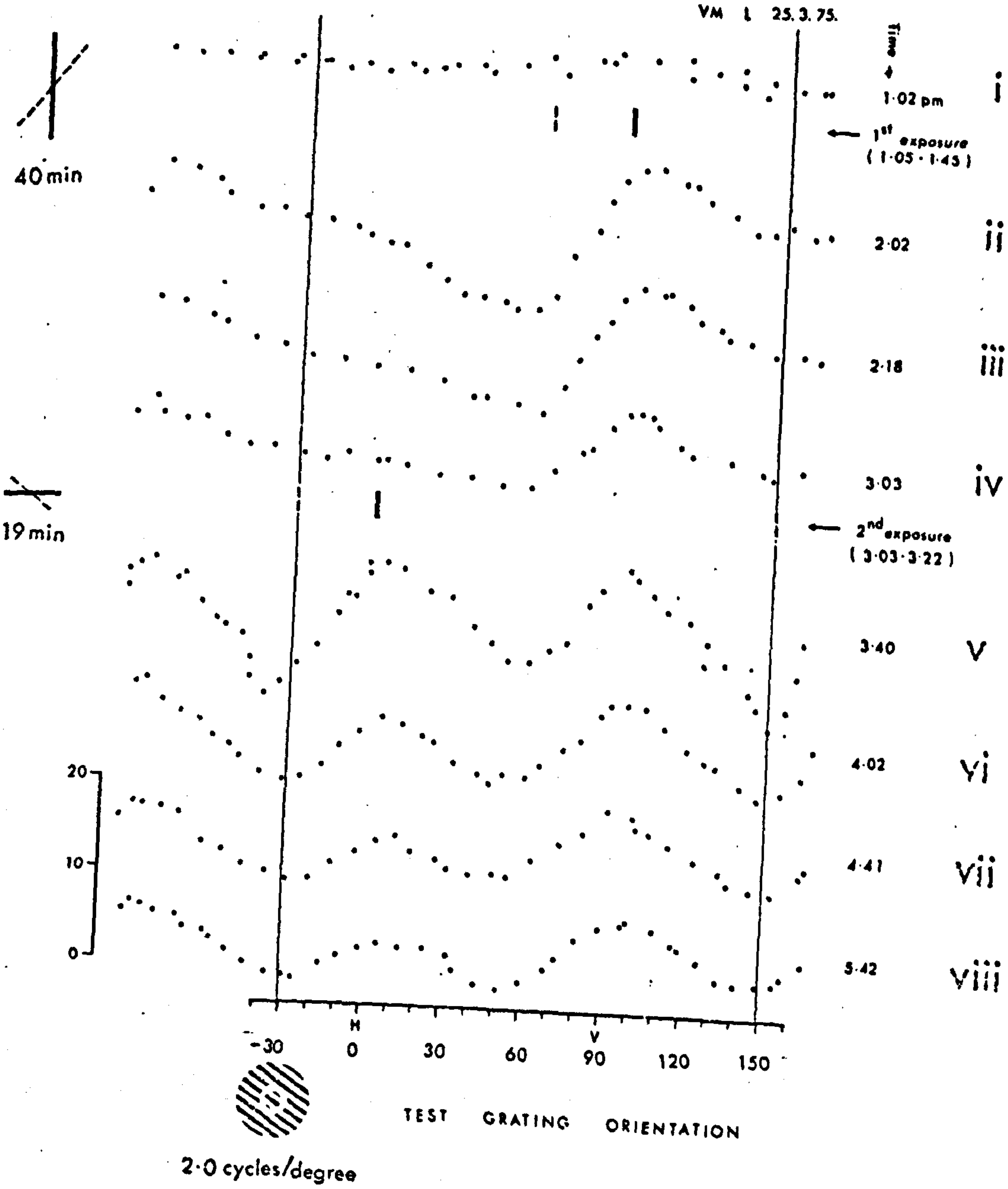

Figure 39 Experiment 8.2.3

a) Angular distributions of OCCA measured at times marked on right, throughout a run with a first (40 min) exposure to a pair of red and green gratings at 90° and 60° (1.05-1.45 pm), followed 2 hours later (3.03-3.22 pm) by a 19 min exposure to the same two gratings each turned through a right angle.

control. Thereafter, the subject had a 40 min exposure to alternating red and green gratings oriented at 90° and 60° to horizontal respectively. After 10 min in darkness, distribution (ii) was obtained, showing the expected bimodal curve with peaks at about 55° and 100° to horizontal. (Note that in figure 39 results are shown uncorrected for the initial bias of (i)). Successive 7 min cycles of testing, ending at the times indicated, yielded distributions (iii) and (iv). Between test cycles the subject was in a normally lit laboratory environment with white walls of luminance 34 mlm. One hour after the end of the first exposure period, the subject had a 19 min exposure to the second pair of red and green gratings, oriented at 0° and - 30° to horizontal respectively.

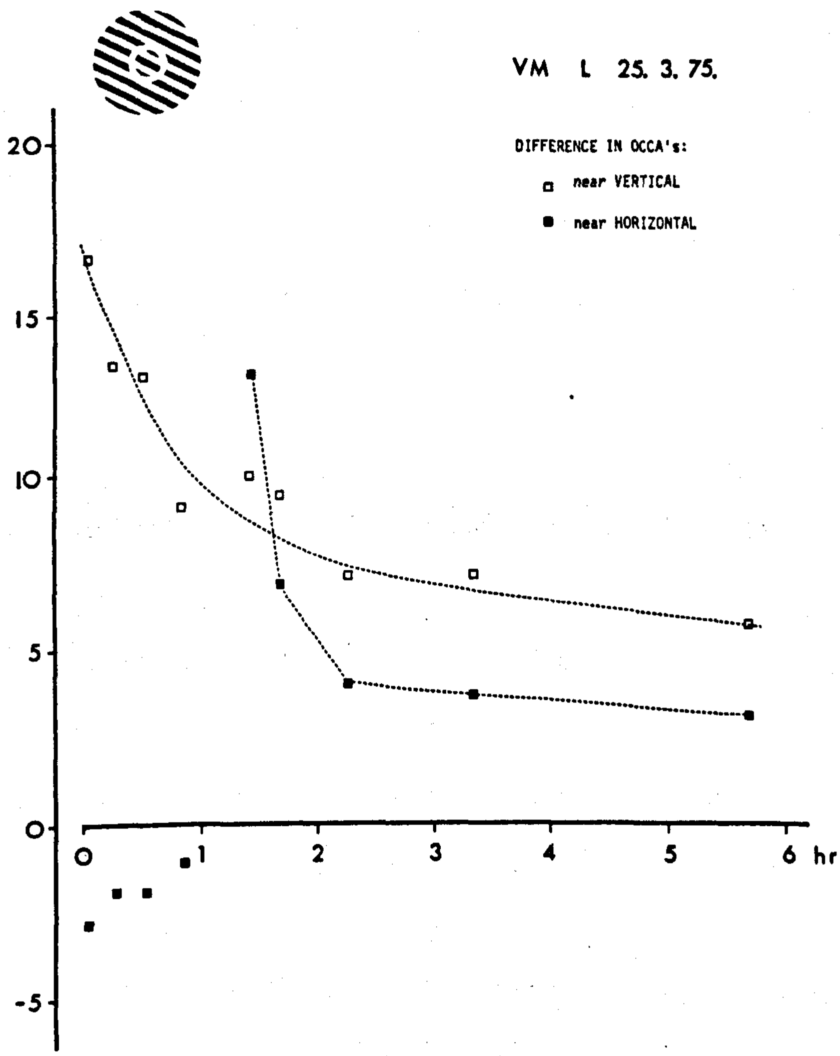

Figure 39 Experiment 8.2.3

b) Peak to peak amplitudes (□ near vertical, ■ near horizontal) of the distribution functions shown in a), against time in hours.

After a further 10 min in darkness, distribution (v) was measured. This shows the newly induced maxima at about +10° and -35° to horizontal, with an initial peak to peak amplitude greater than the residual peak to peak value of the first aftereffect.

Figure 39b shows the peak to peak magnitudes for the aftereffects near vertical and near horizontal plotted on linear coordinates as a function of time spent in the light. These same peak to peak magnitudes are replotted on log/log coordinates in figure 40 with time origin at the opening of the eye a) after the first exposure, b) after the first, second exposure respectively for the aftereffects near vertical, horizontal. Parts c) and d) of figure 40 show plots corresponding to a) and b) above, for one of three further runs performed under similar conditions but with readings taken only at those orientations where the aftereffects peak. Table 20 summarises the results of the log/log plots corresponding to figure 40b for all four runs. A run on another subject showed, though with a large scatter, approximately the same features.

Findings: At least for one subject, the earlier and later aftereffects at different orientations in one eye have been found to decay at different rates. This is particularly clearly the case at the point where the two aftereffects cross over (figure 40 b and c).

The second exposure transiently disturbs the readings for the first; in three runs this reading was raised and in the fourth (figure 40 c) lowered. Nevertheless the general course of each aftereffect has to a first approximation (figure 39b and figure 40) that shape which we have met in chapter five for the usual McCollough effect with origin after the end of the appropriate exposure. The values of β (table 20) for the aftereffects at the separate orientations fall within the usual range.

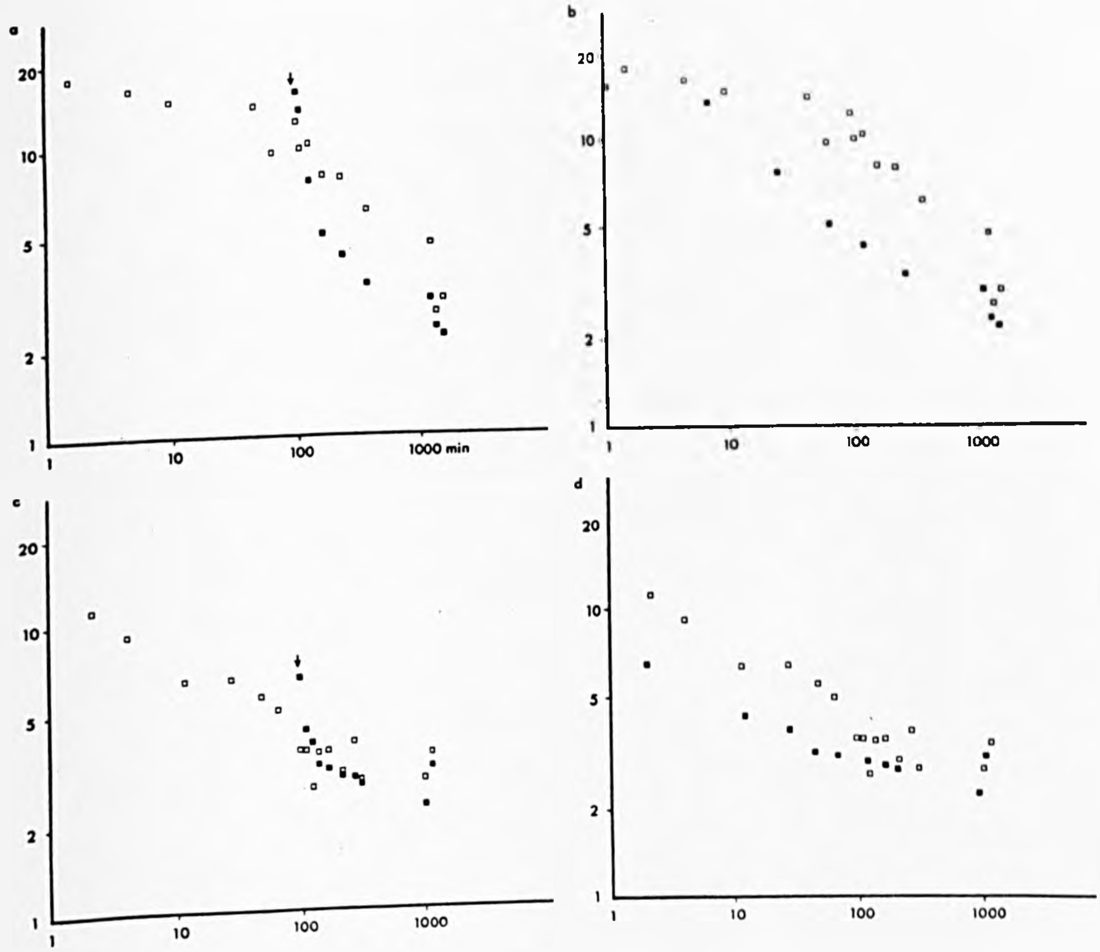

Figure 40 Experiment 8.2.3

The peak to peak magnitudes, a and b, from figure 39 ; c and d from a similar run in which the second exposure lasted 15 min, plotted as a function of time on logarithmic coordinates.

In a and c the time origin is at the opening of the eye after the end of the first McCollough exposure; in b and d the time origin for the aftereffects near vertical and horizontal is at the opening of the eye after the end of the corresponding McCollough exposure. In figure 40 a and c, the arrow indicates the end of the second exposure. In figure 40 b and d T_o differs by 1½ hours for the two sets of results on each graph.

Table 20 The decay of the two aftereffects induced by McCollough exposures at different times and different orientations in the same eye

Date	The exposure to near-vertical stimuli			The exposure to near-horizontal stimuli		
	Duration in min	T_o^v Time of opening eye after end of exposure	Slope, β, of log/log plot - with origin T_o^v	Duration in min	T_o^h Time of opening eye after end of exposure	Slope, β, of log/log plot - with origin T_o^h
9 Sept. 1975	40	1.40 p.m.	0.24	10	2.52 p.m.	0.32
2 Sept. 1975	40	3.51 p.m.	0.26	15	5.26 p.m.	0.19
25 March 1975	40	1.51 p.m.	0.19	19	3.32 p.m.	0.28
30 June 1975	40	10.50 a.m.	0.19	23	12.27 p.m.	0.17

The left eye of one subject, VM, was used in all runs. The time between the start of the first and second exposures was in each case close to 140min.

Discussion: Complete independence of the aftereffects of pairs of gratings cannot be expected in this experiment even in the absence of lateral inhibition. Because of the very broad angular spread of each aftereffect, the maxima produced by each set of gratings separated by 30° from each other fall in positions where the effect of the other pair has about 11% of its maximum value. If simple summation holds for these effects, we should therefore expect a steepening of the decay of the first aftereffect after the second has been added, and a gradual decrease with time in the rate of (log/log) decay of the second aftereffect. These features are each indeed observable in three of the four runs.

Conclusion: Aftereffects at different orientations in a single eye pursue decay courses which are, at least to a first approximation, independent.

8.3 Chromatic aftereffects contingent upon curvature

Riggs in 1973 reported, 'Curvature-dependent colored aftereffects have been established'. After about 10 min of alternate fixation of 'the centers' of patterns of curved gratings (like those of figure 41) projected in red and green light respectively, his subjects reported seeing 'a coloration that was opposite to the one in the corresponding curved lines during inspection' on achromatic test fields like figure 42 When subjects were asked to rank the 'vividness' of the coloured aftereffects which appeared on a set of such test figures having curvatures greater and less than that of the inducing figures they 'all saw more definite coloration on the panels of stronger curvature' than on the panel whose curvature matched the inducing stimuli. Riggs considered the possibility that the effects he has 'attributed to curvature may instead arise from the differences in orientation or tilt that are present . . . in the red and green inspection patterns . . . increasingly . . . as the curved lines run out to the left and right edge of each pattern' from the central fixation point. But he dismissed this 'oriented line hypothesis' on the following three grounds (Riggs, 1973, 1974; and in Stromeyer and Riggs, 1974):

1) Firstly, that the horizontal middle portion of the curves, though not tilted at all, appeared coloured.

2) Secondly, that colour specificity was retained when the subject moved his gaze to other parts of the pattern during testing, and was still seen 'when only a 2^{o} strip of the $5\frac{1}{2}^{o}$ test pattern was disclosed in testing.

3) And thirdly, that 'the most vivid aftereffects are seen on the test patterns having a stronger curvature' than the inspection patterns.

This third - and at first sight strongest - ground for postulating curvature- and angle- (White and Riggs, 1974) detectors has been independently criticised by Stromeyer (Stromeyer and Riggs, 1974), MacKay and MacKay (1974, 1977) and Sigel and Nachmias (1975) all of whom have argued along the lines indicated in 8.2.2, and have also experimentally demonstrated, that after a McCollough exposure to <u>straight</u> red and green gratings making only a small (c. 12^{o}) angle to each other, a 'repulsion of the chromatic maxima' by 12-30^{o} in testing is to be expected and is observed. (Cf. experiment 8.2.1.)

In reply to Riggs's (1973) first two points Stromeyer (1974) has said that these features could be expected from the McCollough effect's known combination of retinal specificity with a tendency to generalise by about 3^{o} (Stromeyer, 1972) (see sections 2.5.1.5 and 2.6). I consider that these latter considerations adequately account for all further similar points made by Riggs (1974) in reply to MacKay and MacKay (and included under 2 above for brevity). As further support for the oriented line hypothesis both Stromeyer and MacKay and MacKay have independently remarked on the 'clear reversal' of hue that they observed with fixation, during testing, at a degree or more outside the vertical edge of the pattern.

8.3.1 To isolate the curvature-contingent chromatic aftereffect

However, the fact that all the qualitative facts observed by Riggs were to be expected from the properties of the McCollough effect does not prove that there is not, in addition, a curvature contingent effect. Only by performing a control experiment in which the exposure to coloured oriented stimuli is identical in duration for each part of the retina exposed, can a curvature- (or angle-) contingent effect be isolated. Such control experiments were performed independently by Stromeyer,(in Stromeyer and Riggs, 1974) and MacKay and MacKay (1974).

Stromeyer's (Stromeyer and Riggs, 1974) 5 subjects tracked moving fixation lights across the stationary coloured curved patterns through an excursion of nearly four times the pattern width. Thus a region of the retina equal to nearly twice the pattern width received an unbiassed orientational diet (though regions to left and right of this did not). No chromatic aftereffect was seen on the test pattern with gaze anywhere within the test contours even after up to an hour of exposure.

In order that the average times spent by the pattern on each part of the retina should be exactly equal, MacKay and MacKay (1974) instead of moving the eyes moved the curved coloured patterns uniformly to and fro during fixation of a stationary light. Experiment 8.3.2, below, appears as cases II and I in MacKay and MacKay (1974). Case II is the adequately controlled situation. It uses a pattern excursion of twice the pattern width a, but the pattern is allowed to appear on the screen only within a region around the fixation point equal to the pattern width. Case I can be regarded as a control of this control since it tests whether pattern-contingent effects can be readily obtained using this type of moving pattern as stimulus. It uses a pattern excursion equal to the pattern width. An excursion of this size has been used and defended by Riggs (in 1974, in Stromeyer and Riggs (1974) and White and Riggs (1974)). That it does not at all supply an orientationally unbiassed diet to each part of the retina (even within a middle strip equal to the pattern width) has been argued in MacKay and MacKay (1974) and can easily be appreciated by considering the successive tilts seen by a point on the retina which receives one edge of the pattern when the pattern is at the middle of its swing. Only one direction of slope is ever seen by this point.

Experiment 8.3.2 To isolate the curvature contingent chromatic aftereffect

Inducing stimuli: An upward and downward curving grating (figure 41 a, b) were presented alternately on a screen in an otherwise darkened room. The two slides were paired with a red and a green filter (cinemoid 14, one layer; cinemoid 24, two layers) and had a luminance of 0.3 log ft Lamberts in the coloured areas. The patterns of figure 41 a and b subtended $6.3^{\circ} \times 7.2^{\circ}$, $2.4^{\circ} \times 2.7^{\circ}$ respectively at viewing distances of 1 m, 2.5 m respectively. Their grating subtenses were respectively 2.8, 4 cycles/degree and radius of curvature 1.9°, 3.5°.

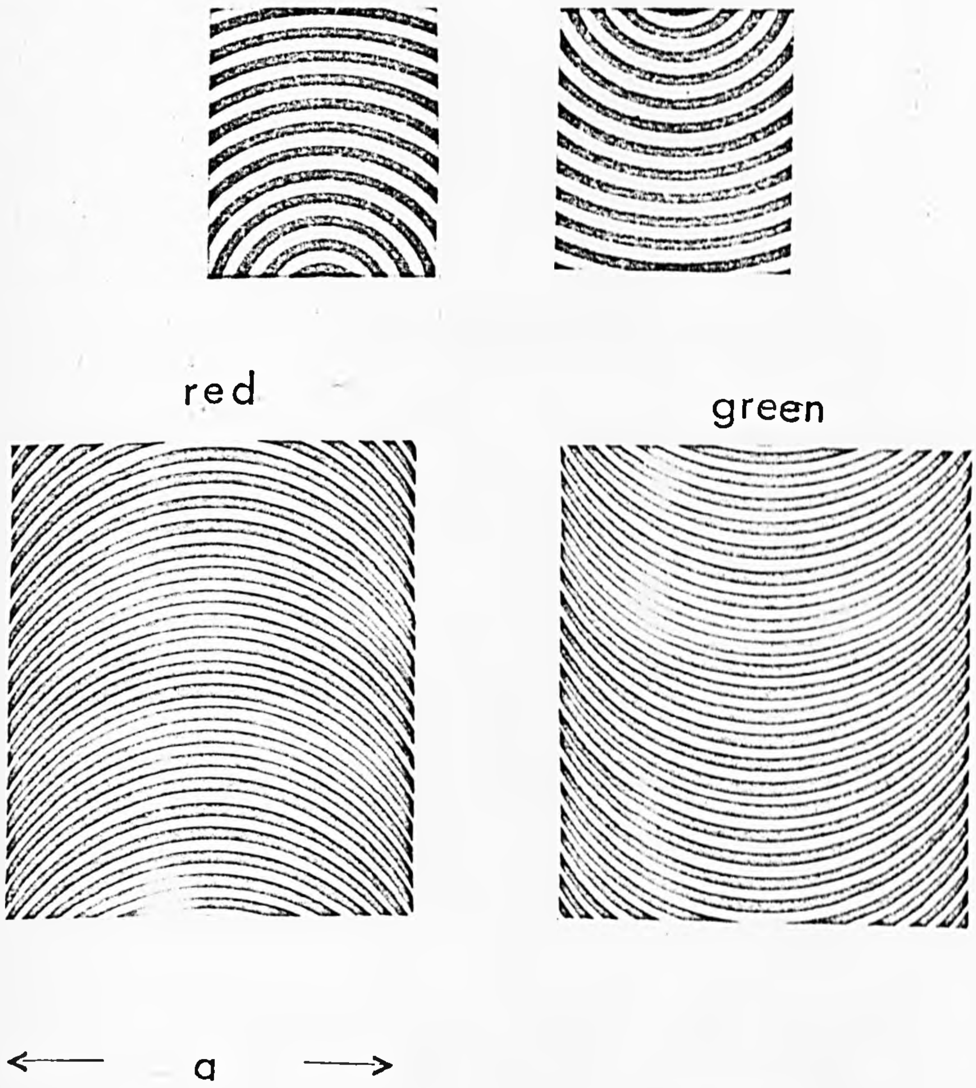

Figure 41

The coloured inducing stimuli used for investigating curvature-contingent chromatic aftereffects. Average radius of curvature, at the viewing distance used, a. 1.9°, b. 3.5°.

An electrically oscillated mirror close to the projector lens reflected the beam to the screen and imparted a horizontal symmetrical sawtooth motion of controllable amplitude and period. Three excursicn amplitudes were used, a, 2a and 0, where a is the pattern width. These are distinguished as Cases I, II and III. For case II two black cards standing vertically at either side of the projector beam ensured that only an area of the screen equal to the width, a, of the inducing pattern received the image.

In all three cases a dim fixation light shone through a small hole exactly in the middle of that part of the screen occupied by the pattern. (In testing, the subject viewed the midline of the test figure.)

Periods of oscillation between 10 and 24 sec were used and gave similar results.

The corresponding achromatic test figures, figure 42 a and b, were viewed from 60, 75 cm respectively in the measuring apparatus M_1. The two central areas of figure 42a were translucent and were rear lit by the colour mixer. The luminance of the test figures was 0.5 log ft L.

Results: Table 21 shows the measured and verbally reported change in the pattern contingent chromatic aftereffects for the three cases in runs of increasing duration using stimuli and test figures of increasing curvature.

Findings: Curvilinear gratings which induced definite chromatic after-effects when viewed for only a few minutes either at rest or moving through an excursion equal to the pattern width (cases I and III), nevertheless yielded no significant aftereffect after an hour's viewing under case II conditions, i.e. when moved to and fro through 2a so as to present all parts of the pattern for equal times to each part of the retina that was to be subsequently exposed to the test figure.

Conclusion: If there is a genuinely curvature-contingent chromatic after-effect it is so weak that it is not visible after an hour's exposure to curved coloured stimuli, i.e. it is more than an order of magnitude weaker than the normal McCollough effect.

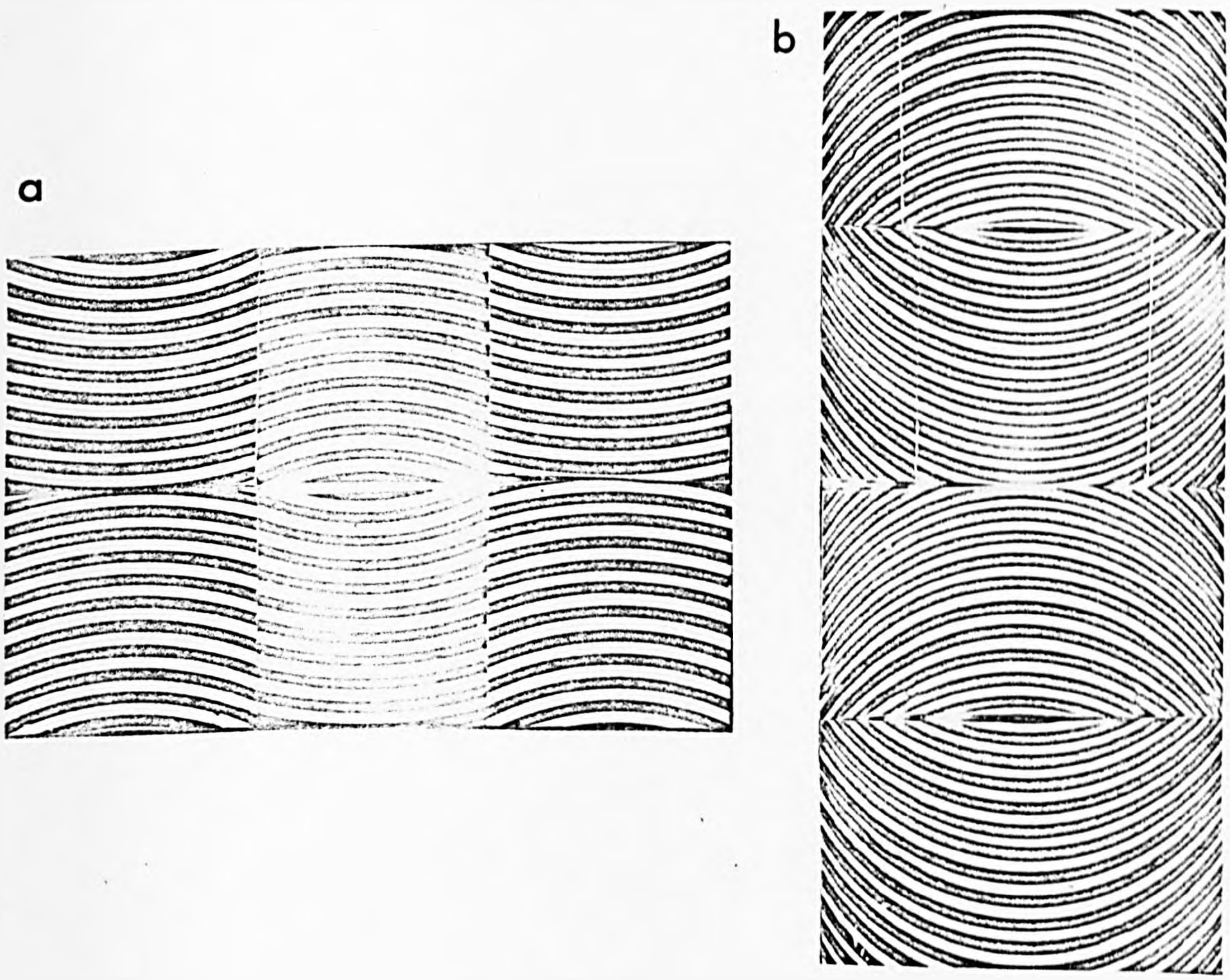

Figure 42

Test figures used for observing curvature-contingent chromatic aftereffects.

Table 21 Pattern contingent chromatic aftereffects

S	Date	Exposure: Case	Exposure: Amplitude	Exposure: Duration (min)	Exposure: Stimulus; radius	Test: Test figure	Test: PCCA Before L	Test: PCCA Before R	Test: PCCA After L	Test: PCCA After R	Test: Change in PCCA L	Test: Change in PCCA R	Test: Change in PCCA Verbal report
DMM	16.11.73	II	2a	10	red concave up; 1.9°		.05	0	.10	-.02	.05	-.02	-
DMM	16.11.73	III	0	10	"			.1		.43		+.33	-
DMM	16.11.73	II	2a	20	green concave up; 1.9°			-.03		-.07	+.4	-.04	-
DMM	16.11.73	III	0	23	"			+.03		-.3		+.27	-
VM	29.11.73	III	0	16	red concave up; 1.9°		.02	.02	.42	.21	+.4	+.2	definite pink on concave down
VM	29.11.73	II	2a	60	"		.22	.1	.16	.16	-.06	+.06	nothing
VM	1.1.74	II	2a	44	green concave up; 1.9°		.15	0	.1	.15	-.05	+.15	nothing
VM	1.1.74	I	a	20	"		.1	.15	.6	.63	+.5	+.52	definite pink on concave up
VM	7.2.74	II	2a	60	red concave up; 3.5°		-	-	-	-	-	-	nothing
VM	7.2.74	III	0	5	"		-	-	-	-	-	-	definitely coloured effects

8.4 Summary: The simplicity of the McCollough effect's angular distribution

Some of the literature on pattern-contingent chromatic aftereffects contained suggestions that single coloured gratings produced complex aftereffects at all angles, and that there was interaction between inducing gratings or parts of gratings at an angle to each other. Control experiments offer alternative simpler explanations of the reported phenomena and show that the McCollough effect, so far from being complex is very unsophisticated. There is no sign of an 'orthogonal opponent colour effect', of lateral interaction or of a curvature-contingent effect. The aftereffect produced by a single straight coloured grating is solely of the complementary hue. It extends to some 65° either side of the inducing grating's orientation with a near Gaussian distribution function for which $\sigma = 21^{\circ} \pm 3^{\circ}$. Exposures to more than one grating yield nett aftereffect distributions which are simply the arithmetic sum of the effects produced by the individual gratings.

Chapter 9 Possible Mechanisms and Loci for the McCollough effect

By 1972 three quite different - though not necessarily competing - explanations of the contingent aftereffects had been put forward. As we have seen in chapter 1 these were in terms of 'normalisation', conditioned responses and the adaptation of single cells (chapters 1.3, 1.4, 1.15.2). These ideas will now be reviewed in the light of more recently available data and especially as they apply to the McCollough effect. Some more recent physiological suggestions will also be touched on.

9.1 The idea of Normalisation seems as applicable now to the McCollough effect as it was in 1972 - perhaps even more so. For the long time constants since reported are well suited to the task of removing from attention the persistent (and therefore uninteresting) aspects of an environment whose statistical uniformity is evident only on a rather long sample. And the cessation of bias adjustment in darkness seems a very appropriate feature to find in a mechanism for centering the working range of the system on the average properties of the visible environment.

If we ask what practical advantages accrue from the normalisations effected by the contingent adaptations, the most convincing example is the prism aftereffect. It gradually renders invisible, at average luminance levels, any persistent chromatic aberration in eye or spectacles, while retaining acceptably clear perceived contours (cf. MacFarland, 1883 who evidently pursued his profession as an ocular surgeon wearing 7^{o} prisms). In the case of the various motion aftereffects, a parallel account in terms of normalisation would presumably say that in walking through a textured, coloured, etc. environment we are rendered less conscious of our own movement and thus more sensitive to movements of objects within the environment relative to one another. When we are stationary, the adjustment to the average combinations of colour, texture, etc. renders us more sensitive to those slight differences of colour etc. which reveal the presence of, for example, a basking snake or underground water in the desert.

9.2 Conditioned responses, memory and the contingent aftereffects

Two aspects of the contingent aftereffects have led particularly to their being likened to memory and learning of the conditioned response type; their remarkably long durations, and the fact that what is stored is in each aftereffect an association of two features extracted from the regularities of past history.*

In order that the resemblances of the contingent aftereffects to associative memory may be assessed, eleven of the principal characteristics of conditioned responses and of memory are listed in Appendix IV. The corresponding properties of the contingent aftereffects are grouped under the same headings in 9.2.1-11.

9.2.1 Wide range of stimuli

The stimulus parameters which can be paired to produce contingent aftereffects seem to be limited in number to about seven. Mayhew and Anstis have remarked, that even so apparently simple a stimulus as small discs and small triangles moving in opposite directions, generates no form contingent aftereffect. (1972.) Those parameters which do produce aftereffects have nothing obviously motivational about them.

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* The papers which emphasise the similarity of the contingent aftereffect to conditioned responses and to memory include Murch, 1971, 1977; Mayhew and Anstis, 1972; Leppmann, 1973; Skowbo, Gentry, Timney and Morant, 1974; Creutzfeldt, 1975.

9.2.2 Positive response

Following induction in which two stimulus parameters (e.g. colour and orientation, colour and movement) are presented simultaneously, the contingent aftereffects are negative. Presentation of the two parameters sequentially can lead to positive or negative aftereffects according to the order in which the parameters are presented (Murch, 1976, see 9.2.5 below).

In the case of the McCollough effect somewhat ad hoc ways have been devised of interpreting the negative aftereffects as in fact evidence of a positive 'response'. Skowbo et al. (1974) suggested that the fatigue (and not the firing) of the colour units is the conditioned response elicited by the oriented line stimulus. Murch (1976) has similarly proposed that the conditioned response is 'the same shift in chromatic sensitivity that the color stimulus produced in inspection'. Leppmann (1973) suggested that an opponent colour response occurs. (This last explanation is not readily extensible to the non-chromatic contingent aftereffects - unless we are to suppose that the systems mediating tilt, polarity of contrast, direction of motion stereoscopic depth all contain suitable linkages between 'opposites'.)

9.2.3 Interocular generalisation

No appreciable transfer of a contingent aftereffect to an occluded eye has yet been reported. There is also very little generalisation to unstimulated areas of the exposed eye (see 2.6). Opposite pairings of two parameters can be simultaneously induced in the two eyes with no loss of aftereffect strength (Hajos and Ritter, 1965, 1.2.7) and even in two areas of the same eye (Harris, 1969, 1.5.1.5).

9.2.4 'Transposition'

Mayhew and Anstis (1972) found evidence of transposition for each of the three motion contingent aftereffects which they investigated. The experiment of Stromeyer (1972b) described in section 1.6 can also be interpreted as an instance of transposition - the single grating of intermediate spacing appearing finer or coarser and consequently also pinker or greener according as coarse or fine gratings have been viewed in the immediately preceding Blakemore and Sutton adaptation.

I have already (in chapter 1.1, 5.2) suggested that in each of these cases an explanation can be offered in fairly peripheral terms.

. On this view transposition is the result of adaptation of parts of the input channel to colour, spacing or luminance, and has no necessary connection with the later processes of memory, association or conditioning. (This is not of course to deny that generalisation of a more sophisticated kind may occur centrally in other tasks and as part of the memory process.)

9.2.5 Delayed, simultaneous and backwards conditioning

Murch (1976) has performed experiments on the McCollough effect in which he has regarded 'the lined grid . . . as the conditioned stimulus (CS) while color functions as the unconditioned stimulus (UCS)'.

In his experiment 1 both stimuli were in fact seen simultaneously for 4½ sec out of a 6.5 cycle but the onset of either stimulus could occur up to 1 sec before the other. The strengths of the chromatic aftereffects were estimated by the subject (on a self-set number scale) at regular intervals during three min of exposure to the McCollough-type stimuli. Strongest effects were reported under the 'simultaneous conditioning' situation and slightly weaker ones with 0.5 sec delay in 'forward conditioning'. Other conditions yielded considerably weaker effects.

In Murch's experiment II the two stimuli were not simultaneously visible. They were each presented for 5 sec with a variable dark interval. Stronger aftereffects were obtained when there was no dark interval than when the interval was 0.5 sec. With 'backwards trace conditioning' (i.e presentation of the lined grid following that of the colour) the aftereffect colours were nearly as strong, but reversed! Murch himself concludes that 'the evidence for trace conditioning of the McCollough effect is extremely weak', and suggests that it is the ordinary chromatic aftereffect of the coloured stimulus which becomes associated with the lined grating since these two stimuli partly overlap in time. The importance which Murch thus ascribes to simultaneity of presentation is at variance with one of the most characteristic features of conditioning experiments which is that the two stimuli do not need to be simultaneous in order to become associated.

Overall, Murch's contention that 'the demonstrations presented here show the feasibility of considering McCollough effects in terms of classical conditioning' only just scrapes by: the demonstrations do not cry out for such an interpretation.

9.2.6 The 'potentiation of habituation'

Murch has claimed that 'once the (McCollough) effect has been established and decayed repeatedly, very few stimulus presentations are required to return the effect to full strength'. Hepler found that by persisting in giving her subjects half hour exposures to moving chromatic stimuli on as many as eight successive days, a perceptible chromatic aftereffect was at last acquired.

The results of experiment 5.8.1 (figure 20) of this thesis reveal a similar feature, but at the same time suggestasimple interpretation in terms of the long duration of the aftereffect: progressively shorter exposure times suffice to establish a given aftereffect strength because the relics of earlier aftereffects are still dying away for up to 5 days from induction. The latter provide the base level to which the fresh aftereffect is added. There is no indication in the results of experiment 5.8.1 of increased receptiveness to the McCollough stimuli as the week proceeds. Indeed in over 4 years of viewing coloured gratings I find no obvious increase or decrease in my receptiveness and cannot support Murch's remark that 'experienced observers require only one or two presentations of the chromatic inspection stimuli to re-establish the full McCollough effect'!

9.2.7 Resistance to ordinary forgetting

The claim that the contingent aftereffects last for a month seems to have originated with Stromeyer and Mansfield and has often been reiterated. Stromeyer and Mansfield's four subjects were exposed in two groups to opposite pairings of colour and direction of motion of the stripes. They were tested immediately after the 10 min exposure and when retested 5, 6, 18 and 28 days later still 'saw the aftereffects' when the direction of stripe motion was reversed though more and more briefly. Stromeyer (1971) found that following a 2 hour exposure the McCollough effect was visible for two weeks. I have found in 5 subjects that with very brief inspection of a test card (without measurement), once every day, the aftereffect of a 20 min McCollough exposure lasted 5-7 days. Jones and Holding have claimed that when the McCollough aftereffects produced by a 15 min exposure were not tested at all they 'remained at better than half strength' for 3 months. Moreover they have asserted that a single test session serves as an 'extinction trial' which initiates decay of the aftereffect. If these last statements held up they would be strong evidence for a parallelism with conditioned responses, but (as already described under experiment 5.6) both Keith White and I have been unable to replicate their findings using periods of up to 7 days. It has been remarked above that Jones and Holding's criterion of 'full strength' was derived from a different group of 10 subjects and that the effects being measured are comparable with the differences between subjects. Jones and Holding themselves comment on the 'noisiness' of the measurements obtained from the 4 groups (of 10 subjects each) whose first test fell upwards of 10 days after exposure.

Two comments may be made concerning the observation of aftereffects weeks and months after induction. The first is that the normal environment is full of stimuli which will be generating fresh small contingent aftereffects. In the case of the McCollough effect, if the subject is astigmatic or wears glasses which slightly over- or under-correct the effects of his astigmatism at the particular contrast of the test figure, he will see coloured effects in the spaces between the black lines which are indistinguishable from a McCollough effect. That such effects are not negligible is shown by Stanley and Hoffman's (1976) report that subjects who had never intentionally been exposed to McCollough stimuli gave persistent reports of seeing colours on an achromatic test field.

The second point is that after a little experience of seeing small aftereffects, the subject becomes much more observant of - and prepared to mention - other small effects which look the same but are caused by eye movements or astigmatism.

In summary, it can safely be stated that the McCollough effect lasts for 1-2 weeks.

9.2.8 Extinction

Mayhew and Anstis (1972) found that the motion aftereffect contingent upon colour was 'remarkably resistant to extinction' (by 15 min periods of viewing coloured stationary fields and 2.5 min of achromatic moving fields). 'Even though after repeated exposure to the test fields the CMAE would decrease and even disappear, it would reappear after a short rest' (2 min in dark) and was still visible by 2 out of 4 subjects 2 days later.

The McCollough effect is also fairly resistant to extinction. Skowbo, Gentry, Timney and Morant (1974) and MacKay and MacKay (1975b, 5.3.3) have reported that the McCollough effect decays faster if the subject continuously views an achromatic grating instead of the normal environment between measurements. After 10 min of such viewing most illusory colour disappears from the achromatic test gratings. But the colour reappears after 5 min in the light (Skowbo and Clynes (1977) and experiment 5.3.3.1). These results are possibly explicable in terms of the overlaying of the original McCollough effect by later aftereffects, McCollough and otherwise; possibly also in terms of the depletion and subsequent recovery of chemicals at synapses (9.3.1.11)

Jones and Holding (1975) have claimed that one test with a field of gratings is sufficient to initiate a decay process and that decay is otherwise very much slower, but I have not found that testing 'triggers' decay (5.7).

9.2.9 '<u>Spontaneous recovery</u>'

The preceding section described reappearance of contingent aftereffects following 10-30 min spent in viewing the 'unconditioned' stimulus. A second instance of 'spontaneous recovery' is afforded by the weak return to an earlier McCollough effect within about half an hour of receiving a 'neutralising' exposure to coloured gratings (e.g. experiment

5.8.1). As shown in chapter 5.8 this latter type of recovery may be regarded simply as a consequence of the aftereffects' long duration and additivity.

9.2.10 'Disinhibition'

So far as I am aware there have been no reports of a strengthening of the perception of a contingent aftereffect when presentation of the test figure is accompanied by acoustic or other stimuli.

9.2.11 Decreased rate of forgetting in sleep and darkness

MacKay and MacKay (1975b) have reported that the McCollough effect does not decay when light is excluded from the eye. Skowbo (personal communication, 1974) also finds less decay of the McCollough effect in darkness than in the ordinary environment, although her earlier paper (Skowbo et al., 1974) reported no difference. In a similar way, the motion effect contingent upon polarity of contrast lasted 17 hours when night made up part of that time, but only 7 hours in daylight (VM unpublished Appendix 1). The conclusion drawn from experiment 5.4.1 is that fresh (visual) experience not merely hastens, but is essential for, decay of the McCollough effect.

The resemblance of the McCollough effect to memory in this respect may be counted as one of the few strong points of similarity. It must, however, be remarked that there is nothing exclusive to memory about a decreased rate of decay in darkness. It has been reported, for example, that the ordinary aftereffect of motion can be seen for a few seconds longer if, instead of ordinary visual stimulation, darkness or other states in which novel input is reduced follow induction of the effect. (Wohlgemuth, 1911; Spigel, 1962; Honig, 1969.) The reduction in the visibility of a grating after prolonged exposure to a similar grating (Gilinsky, 1968) persists for more than double the time when in darkness than it does under normal visual stimulation. Certain figural aftereffects are also alleged to fade less during 30 min of viewing a ganzfeld or darkness than in 30 min of exposure of the normal environment. (Pick, Hetherington and Belknapp, 1962).

9.2.12 Summary: Comparison of the contingent aftereffects with memory and conditioned responses

In lasting for as long as a week and suffering little or no decay in the absence of fresh visual input, the contingent aftereffects indeed show a muted resemblance to conditioned responses and memory. The long time course has consequences which resemble 'the potentiation of habituation' and 'spontaneous recovery'. A process somewhat like 'extinction' also occurs - though 'single trial extinction' does not. 'Transposition' occurs but is quite possibly not an integral aspect of the contingent aftereffect's mechanism. The evidence under the remaining five headings does not press a conditioned response interpretation of the contingent aftereffects upon us but rather the reverse. The most prominent difference is that the aftereffects are negative whilst memories are positive.

On the present evidence it does not seem justifiable to class the contingent aftereffects as conditioned responses, though it is conceivable that some similar pieces of neural machinery may be involved in the long storage of information in the two situations.

9.3 Explanations at the physiological level

Celeste McCollough (1965b) invoked the 'adaptation' of colour coded 'edge detectors' to explain both the prism effect and the aftereffect which she had discovered. Since neural units responsive to oriented edges are not found in cat or monkey cortex prior to the cortex, these 'edge detectors' have been generally held* to be cortical neurones of the kind

* E.g. by Fidell, 1971; Wyatt, 1974; and many others including ourselves.

described by Hubel and Wiesel (1962, 1968) - even though only a small fraction of such cells are in fact sensitive to both colour and orientation and only a small fraction are so strongly monocular as the McCollough effect (see 1.4).

Until 1972, the 'adaptation' of these cells was generally thought of as cell 'fatigue' or 'habituation' of the kind which Barlow and Hill (1963) had suggested might explain the motion aftereffect. But as the McCollough effect's extremely long duration came to be appreciated, it was realised that some more enduring modification than temporary chemical depletion or self-biassing must be envisaged.

9.3.1 Synaptic modification

The nervous system is rich, at every level, in lateral linkages between neighbouring cells. A cell's activity presumably influences, and is regulated by, the state of its neighbours within its own level. In 1973 we suggested (MacKay and MacKay, 1974a) that if the synapses of such lateral linkages become modified in conductivity on the basis of coincidences or differences of activity in the two cells which they link, then the network could well show long time-constants in the alteration of its biasses, and a power law time course in which the probability of further modification declines with time. We pointed out that the cells concerned need not themselves be orientationally sensitive. Provided cells have connections with neighbours in various directions such a network will develop orientational biasses in response to a visual input containing oriented stimuli. In the same way, if the intercell connections vary somewhat in length, the network will also develop spatial biasses and show, moreover, exactly the same time constants for acquisition and loss of both spatial and orientational properties (cf. chapter 7.1.1.6). If such modifications of connectivity are indeed responsible for the McCollough effect, there must be either two separate populations of inter-connections between the cells fed from the red and from the green cones, or else colour-opponent linkages between cells in the two groups.

Such a model was prompted by the power law form of the decay curve and the existence of the chromatic aftereffect contingent purely upon spacing. But it also finds a natural place for several features* of the McCollough effect which did not sit easily with the cortical edge-detector explanation. The following properties may be particularly remarked:

9.3.1.1 the bluntness of its orientational tuning (65° spread compared with 15° for cortical cells (8.1.4)

9.3.1.2 its insensitivity to precise pattern detail (1.5.1.4).

9.3.1.3 its strong dependence on contrast (1.2.5, prism a-e 1.5.1.3) and complete lack of dependence on kinetic and cognitive contours (7.3, 2.7.7).

9.3.1.4 the absence of any associated threshold change (2.5.3).

9.3.1.5 its robust stability (cf. Kohler's remarks on the prism a-e (1.2.2) which could be made on the McCollough effect equally).

9.3.1.6 its high degree of monocularity (6.2).

9.3.1.7 its combination of both colour and pattern sensitivity (cf. 1.4).

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* Some of these were remarked on by Gibson and Harris (1968), and their dipole model was designed with them in mind.

9.3.1.8 the many respects in which its properties differ from those of other aftereffects of supposedly cortical origin involving oriented lines (cf. 1.7, 2.7.7).

Most of all, however, it is the temporal properties of the McCollough effect which recommend a synaptic model.

9.3.1.9 Thus the remarkable ability of the McCollough mechanism simultaneously to store detailed information concerning earlier and later aftereffects (5.8) seems to require large parallel populations of modifiable elements. These properties are somewhat easier to comprehend if the synapses rather than entire cells are the store for the delicately changing yet very robust and stable trace. Perhaps one might even speculate that the individual synaptic 'boutons' serve as parallel and near independent channels?

9.3.1.10 The discovery that decay ceased in darkness (5.4) showed that decay - a recovery from 'fatigue' - was not a matter of spontaneous repair, and lent persuasive support to the idea of a modification of synaptic couplings on the basis of visual input. The fact that light alone is necessary for recovery shows that not only during adaptation to McCollough stimuli, but also during recovery, the process of modification proceeds in response to the patterns of activity produced by the visual input. When the input is more coherently patterned (5.3.3) such 'over-writing' is more effective (MacKay and MacKay, 1975, 1977a, 1978).

9.3.1.11 Finally the recuperation of the McCollough effect between readings (5.3.4.1) and in darkness (5.5.1), was a feature it was almost impossible to square with a cell fatigue model.* But on a

* cf. Keith White's (1976, p. 36) remarks on the impossibility of retrieving an earlier state.

synaptic model there are probably several ways in which aftereffect hues might spontaneously become stronger without an alteration of conductivity. One might, for example, speculate that, following a period of low visual stimulation, increased conduction at a synapse can occur because a suitable chemical or electrical state has had time to build up at the synapse. The rapid decline of readings during the viewing of an achromatic grating (5.3.4.1 , 5.3.3) would on this view reflect the discharge of the accumulated store.

The synaptic model can also accommodate the prism aftereffect, without further assumptions, as a particular case. One is encouraged to this conflation of the two aftereffects by the similarities of many of their properties including their decay courses (cf. 1.2.3). There is only one puzzling discrepancy; the report that the prism aftereffect is not visible in twilight (2.4.8), though the McCollough effect is.

J. Krüger of Freiburg (1976b) has made some experiments suggested by the above synaptic model and pointed to a possible site in the lateral geniculate body where interneurons would form part of the inhibitory linkage between cells.

9.3.2 Physiological explanations: other authors

A number of other physiological models have been proposed to meet the problem posed by the long duration of the McCollough aftereffect. These all take as starting point the (achromatic) orientation-sensitive cortical units - the pattern channels- and suggest that channels for chromatic information become associated with these by a plastic process akin to that involved in conditioned responses.*

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* E.g. Leppmann, 1973; Riggs, White and Eimas, 1974; Creutzfelt, 1974; Montalvo, 1976; Murch, 1977. (Mayhew and Anstis (1972) make a similar point but in more general terms which do not specify that such features as movement and colour must be first extracted before becoming associated in pairs.)

Several authors have suggested that colour-specific channels from the LGN relay information to orientation specific cortical cells. Creutzfeldt's suggestion as to how this linkage might be engineered is the most explicit: he draws attention to the fact that although the majority of pattern sensitive cortical cells in the monkey are not colour sensitive, a few (orientationally sensitive) cells, sprinkled through the columnar origanisation of area 17, are fed from only one type of cone. These, if capable of inhibiting their neighbours in the column, could give rise to a colour specific bias out of proportion to their own numbers.

9.4 Locus of the McCollough effect

Once we entertain the possibility that synaptic modifications between non-orientationally sensitive cells could be responsible for the McCollough effect, the* locus of the effect is no longer necessarily confined to the cortex and could even be retinal. (MacKay and MacKay, 1973.) Let us then survey the evidence which has a bearing on its locus. (Some has already been mentioned in chapter 2.6 - 2.8.12).

9.4.1 The dichoptic and binocular aspects of the McCollough effect (6.1, 6.3) presumably lie within the binocular pathway. (The non-global transference of colour to the pattern eye in the dichoptic effect (6.1.7.1) seems to rule out a retinal site for any part of the dichoptic effect.) The similarity of the properties of the binocularly and monocularly

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* It is not, of course, necessary to assume that an aftereffect has a site at one level only. B. Julesz (1971) presents evidence that the motion aftereffect probably occurs both before and after binocular fusion, and the experiment of Stromeyer (1972b) seems to demand a similar conclusion regarding the spatial frequency shift.

induced McCollough effects may point to their being located at the same level.

9.4.2 The McCollough mechanism is fed by all four types of retinal receptor (2.4.5).

9.4.3 The McCollough effect is sensitive to pattern contrast and to luminance.

9.4.4 The arrest of decay in darkness suggests that, at the site of the McCollough effect, the level of activity is low in the absence of incoming stimulation by light.

9.4.5 The McCollough effect comes at the same stage of the visual pathway, or later, than the sites of the following effects:-

9.4.5.1 the fading of stabilised images (1.5.1.1) (Leppmann and Piggins, 1973);

9.4.5.2 the persistence of vision (7. 5).

9.4.5.3 simple chromatic adaptation (Murch and Hirsch, 1972; 2.4.6);

9.4.5.4 the monocular spatial frequency shift (Stromeyer, 1972b; 1.6).

9.4.6 The monocular McCollough effect precedes the locus of the following effects:

9.4.6.1 the interocular transfer of the spatial frequency shift (Stromeyer, 1972b; 1.6);

9.4.6.2 simultaneous colour contrast (Stromeyer, 1971; 2.8.4; also 7.4, and probably precedes:-

9.4.6.3 the 'cyclopean' detection of disparities between coloured areas (Julesz, 1971; 2.8.8);

9.4.6.4 It may also be noted that Held and Shattuck's related aftereffect involving orientation and colour precedes the locus of detection of the disparity of tilted lines (Shattuck and Held, 1975; 1.10).

9.4.7 The McCollough effect cannot be induced or detected using cognitive or kinetic contours (2.8.7 and 7.3 respectively). It is probably not inducible using simultaneous contrast colours (7.4)

9.4.8 The McCollough effect is fairly strictly retinally specific (1.5.1.5, 2.6). It is locked to retinal orientation (Ellis, 1976; 2.8.6) and is largely, though not entirely locked to retinal angular subtense (1.6, 2.7.2).

9.4.9 The McCollough effect does not show marked azimuthal differences in strength or in the width of its tuning curve (cf. figs. 34b and 35 of chapter 8.1; see also Simon Hakiel, 1978).

9.4.10 The McCollough effect does not show marked lateral or cooperative interactions between the lines forming angles (8.3.1) or gratings (7.2)

9.4.11 The McCollough effect does not have properties in common with any other pattern specific or chromatic aftereffects (cf. Table 2) except possibly the prism aftereffect (1.2 and Held and Shattuck's effect, 1.10).

The overall picture is of a locus at a relatively unsophisticated level of the visual system probably at a short distance from the primary receptors. The dichoptic and binocular effects require sites subsequent to the meeting of signals from the two eyes. A possible locus, in keeping with all the above evidence, is therefore the lateral geniculate nucleus.

9.5 Conclusion

The traditional explanation of visual aftereffects in terms of 'fatigue' (2.5) seems to be inapplicable to the contingent aftereffects. The McCollough effect's temporal properties, particularly its lack of recovery in darkness and its accelerated recovery during exposure to patterned light, point rather to a process of adjustment in response to the regularities of the visual environment. The modification of synaptic conductivity between neighbouring colour sensitive cells (possibly in the LGN) has been proposed as a mechanism which would fit with all the known data.

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Appendix 1: A texture-dependent aftereffect of viewing unpatterned colour

When one has viewed an unpatterned coloured field for 2 min, all surfaces appear for some 2 min to be tinged to about an equal extent with the complementary colour. Thereafter, however, those surfaces patterned at about 5 cycles/degree retain the complementary coloration more strongly than those which have finer or coarser patterning, or none. These latter surfaces can even appear to take on the opposite hue - possibly because of simultaneous colour contrast.

Twelve naive subjects viewed for 2 min an unpatterned green (and later a red) field at 2.7 cd/m^2 and made written reports as to which of a set of black and white abutting gratings of 3-14 cycles/degree (at 10 cd/m^2) appeared most colourful one minute later. Only one subject saw no texture dependent differences in saturation of the pink after-effect and only one saw none for the green aftereffect. The others reported seeing the strongest effect on those gratings which subtended 5.4-6.4 cycles/degree.

The effect can be seen on random as well as on regular texturing. It is much increased by defocussing the patterns.

It is produced by blue and by yellow stimuli including 'pure blue' and 'pure yellow' (474 nm and 573 nm). It can be seen peripherally even when the foveal 6° has not been exposed to the coloured field.

Experiments on one subject suggest that the effect lasts longer after viewing a very intense stimulus, but appears most saturated after exposure to a stimulus at 0 to 1 log ft Lamberts.

The effect reaches its maximum after about 1-2 min of exposure to the unpatterned coloured field. The effect lasts 3-6 min. The time course of decay of the difference in apparent saturation between two areas patterned at 4·3 and 1·8 cycles per degree (figure 43) was recorded using hue matching apparatus (M_3). Figure 44 shows that the decay course is near exponential. Its magnitude and form are the same for all exposure durations of from 1-15 min. The course of decay is not affected by closing the eyes. (There is, however, a tendency for most subjects to see more finely textured surfaces as pinker after even brief periods in darkness. Some see them as greener.)

Figure 43 Test figures of 4.3 and 1.8 cycles per degree presented alternately in measuring the decay of the texture contingent chromatic aftereffect.

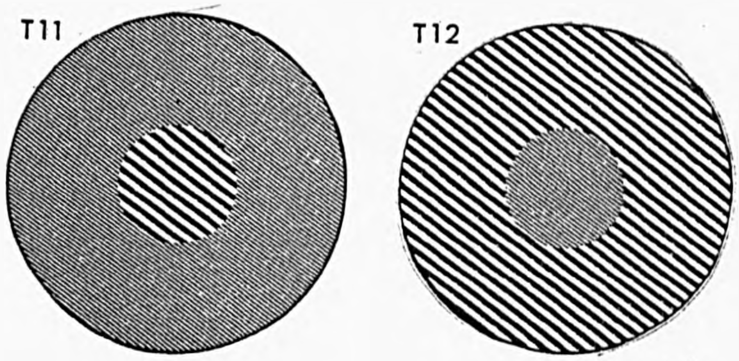
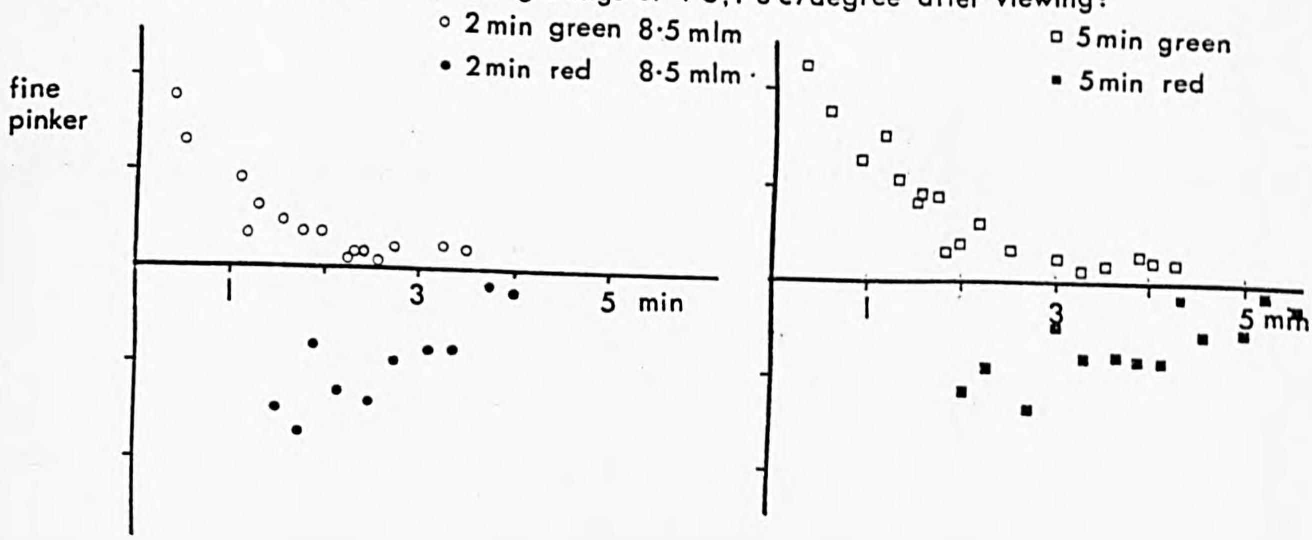


fig 44 Hue difference on test gratings of 4·3, 1·8 c/degree after viewing:



The effect is strictly retinal specific and can be seen even after exposure of only a very small ($\frac{1}{2}^{o}$) region of the fovea to the coloured field. The effect does not transfer interocularly.

This effect is possibly evidence of lateral interaction - perhaps inhibitory - between cells at a peripheral stage of the visual system. The fact that it is most noticeable at about 5 cycles/degree may simply reflect the fact that the visual system is rich in connectivities between cells whose separation corresponds to that average distance.

It may perhaps be also remarked that subjects report that real pale colours also appear stronger when they are laid over patterning of about 5 cycles/degree.

Appendix II: A motion aftereffect contingent upon polarity of contrast

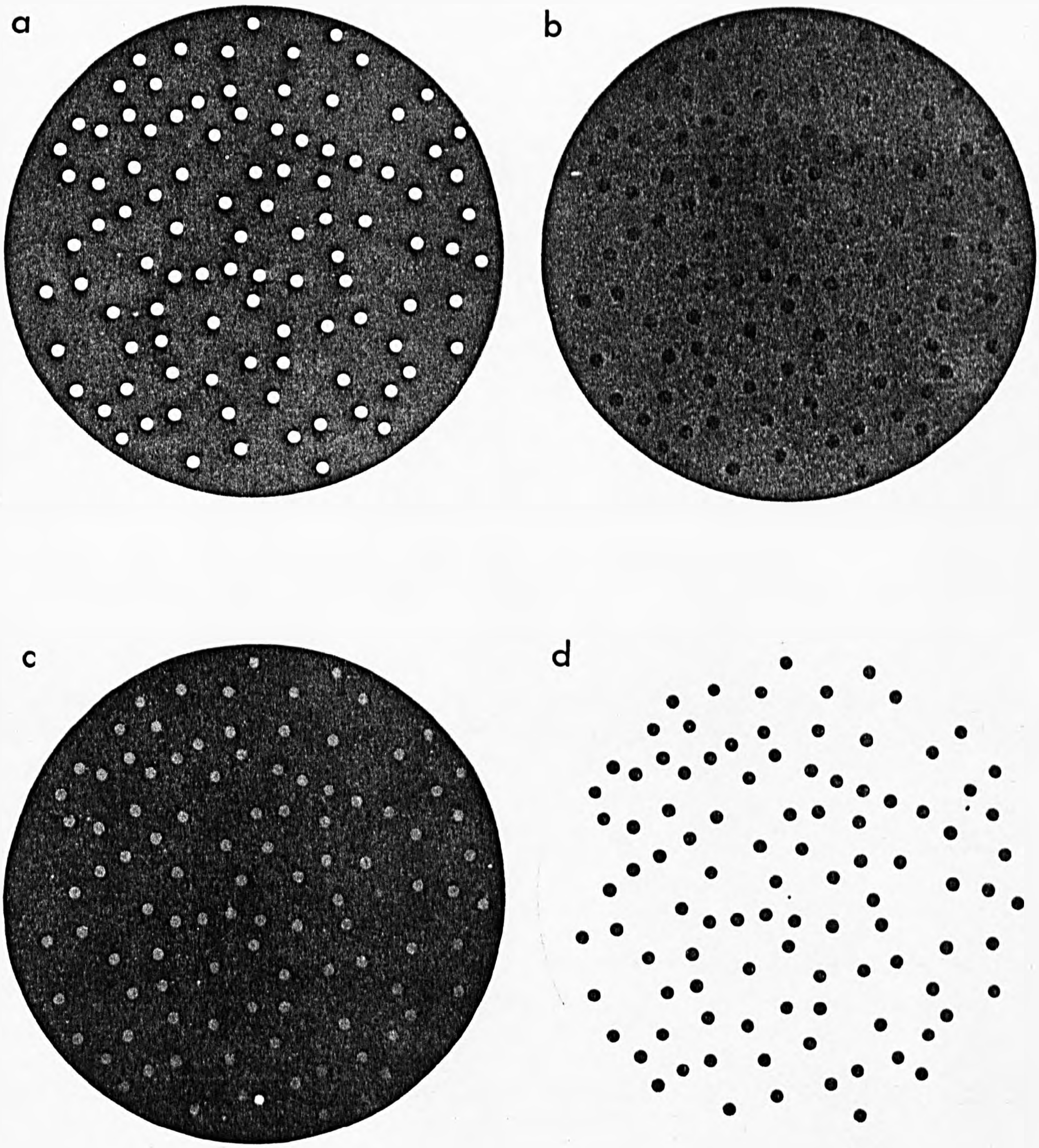
Mayhew (1973) showed that the duration of the ordinary motion aftereffect could be rendered contingent upon the polarity of contrast of a test field by 5 minutes of prior exposure to a pattern and its photographic negative moving in opposite directions (see 1.19).

At about the same time I had been independently making experiments which confirm Mayhew's interpretation of his results as evidence that the motion aftereffect is contingent on polarity of contrast and which add further details. These experiments are reported in this appendix.

The adapting fields consisted of two identical pieces of grey card side by side, each subtending 13° at the observer's eye and bearing a random distribution of 100 circular spots 20' in diameter, white on one card and black on the other. (Fig. 45a and b). The cards were rotated in opposite directions against a stationary grey background at equal rates varying from 4 to 30 sec per rev in different runs. Luminances of the white, grey and black areas were 1.1, 0.9 and 0.1 log ft lamberts respectively. The observer viewed each pattern in turn monocularly through a circular hole (subtending 16°) in a black hand-held card sufficiently large to conceal the other pattern. To reduce the size of associated eye movements he used a rotatable chair and faced each pattern in turn, his eyes being closed for 3 sec between viewings. The patterns were viewed for equal times in the range 3-10 sec, stationary central pencil dots providing fixation points. After 10-20 min of alternate viewings, the rotations were stopped, the observer closed his eyes for 2 min to allow any short-term motion aftereffect to diminish, and then viewed the two stationary patterns alternately. All 4 observers reported definite MAE's in directions which reversed with the polarity of contrast of the test pattern, and were opposite to those originally associated with

Figure 45: Patterns used for adapting and testing.

Following 10-20 min of alternate viewing of a rotating clockwise and b anti-clockwise, a (and c): appeared to move anti-clockwise, b (and d) appeared to move clockwise.



each pattern. These MAE's did not transfer significantly to the occluded eye after 20 min of monocular adaptation.

In case movement of the image across the retina in turning from one test pattern to the other might have been a disturbing factor, I verified that the aftereffect was still visible when using a single reversible-contrast figure: a piece of grey card with holes punched in it at random and either a black or a white card slipped behind it.

This MAE, like other contingent aftereffects, is remarkably long-lasting; following a 20 min adaptation it remained visible for 2-8 hours in a normal visual environment. Moreover, when the inducing exposure was made just before going to sleep the MAE was still strongly visible on awaking 10 hours later, suggesting that its decay (like that of the McCollough effect, MacKay & MacKay 1975b) may be significantly slowed in darkness.

To see in what respects the effect was stimulus-specific, a variety of other test fields were used. Following a 20 min. exposure as described above, no MAE was seen on grey test cards bearing various random mixtures of 100 white and 100 black spots. MAE's were visible on regular square arrays of white or black spots on grey, provided the spots were more than one spot diameter apart; they were visible on a wide variety of random distributions of white or black spots on various shades of grey (0.8 - 1.0 log ft lamberts), and with spots sizes from a half to twice the original; they were still visible at much dimmer and brighter (1.0 - 2.0 log ft lamberts) luminance levels. The MAE's were weak when the test conditions differed most from the original conditions, but it is clear from the above that neither the original pattern nor contrast levels nor luminance level is essential for the two directions of MAE to be visible.

It seemed possible, nevertheless, in view of reports of luminance dependence of MAE's (Mayhew and Anstis, 1972, Sekuler and Ganz, 1963) that the present findings arose simply from the (small) difference in mean luminance between the card with black and the card with white spots. To distinguish between dependence on mean luminance and on polarity of contrast I used a black and a white card each with identical random distributions of grey spots of the same size as above (Fig. 45c and d) in two further experiments. In the first (Expt. A), they served as the test cards after adaptation as above to Figs. 45a and b, and in the second (Expt. B) as the adapting patterns with Figs. 45a and b as the test fields. Except for one null-report by one subject with the white test card (Fig. 45d) in Expt. A, all three subjects reported negative MAE's in every case in directions predictable from the polarity of contrast and not the overall luminance of the figure used.

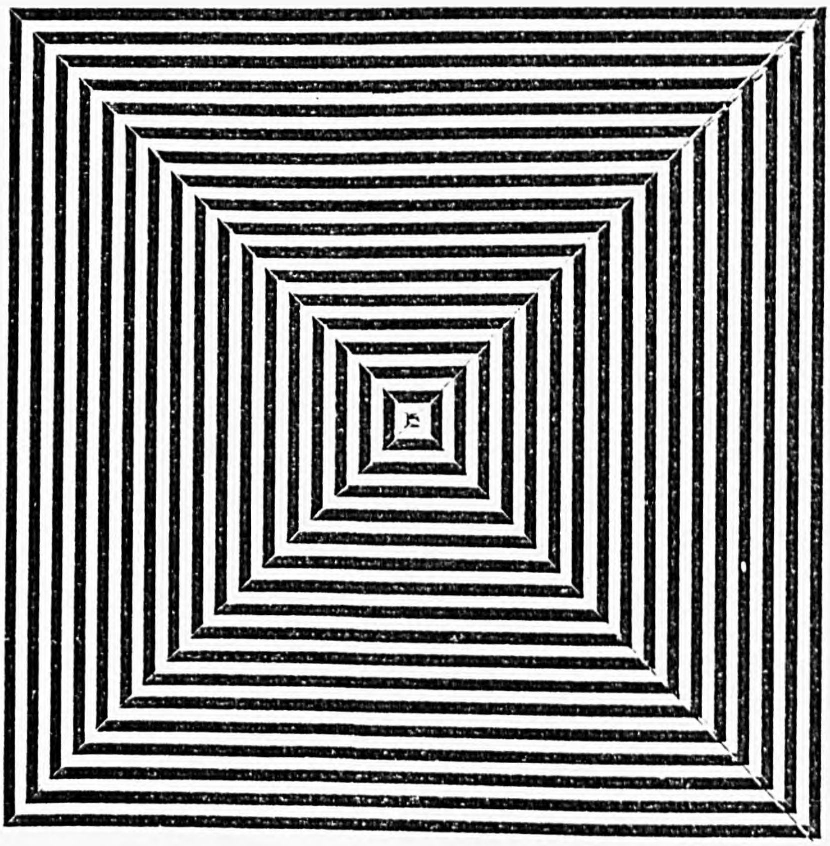
This after effect may be seen as evidence of the B and D systems postulated by Jung (1977).

Appendix III: The effect of boundaries upon perceived saturation and brightness

A pattern of squares nesting symmetrically within each other (figure 46) can be perceived as two alternative Gestalts: either as a set of squares or as four striped triangles. Jenkins and Ross (1977) have reported that when subjects who have a McCollough aftereffect switch their attention from one Gestalt to the other the strength of the chromatic aftereffect seen on the figure is altered. When the figure is perceived as a set of squares the aftereffect hues are weaker than when it is perceived as four triangles.

The following experiment shows that this phenomenon is not confined to illusory hues but is of more general interest.

Figure 46



Triangular pieces of pink transparent filter (Cinemoid 54) or of neutral density filter (of 0.01 log units attenuation) were laid over the two vertically striped triangles of figure 46. The pattern was viewed by artificial light or by day-light (50-300 cd/m^2) at about 50 cm, at which distance the gratings subtended 1.7 cycles/degree and the whole pattern $20^o \times 20^o$. Subjects with no McCollough aftereffect were asked to perceive the figure alternately as squares and as triangles and to report any changes noticed. Without prompting, 3 out of 4 subjects reported that the pink was paler and 3 out of 3 different subjects that the grey was less noticeable when they were paying attention to the squares than when they thought about the triangles.

The phenomenon reported by Jenkins and Ross can be seen using real colours and real luminance differences as well as using illusory hues. It is not, therefore, specifically a property of the McCollough effect. It is possibly related to other phenomena in which colour appears to fill the space within boundaries (Lettvin, 1967).

Jenkins, B. & Ross, J.: McCollough effect depends upon perceived organisation. Perception, 6, 399-400 (1977).

Lettvin, J.Y.: The colours of coloured things. Quarterly progress report of the research laboratory of electronics, M.I.T., 87, 193-22((1967).

Appendix IV: Some distinctive features of conditioned responses and of memory

(1) A very wide range of stimuli can become associated. Unconditioned stimuli which are appetitive or aversive are particularly effective (Hall 1976).

(2) Traditional conditioning theory regards a positive response to the unconditioned stimulus as normal. Thus, after suitable training, Pavlov's dogs salivated upon hearing the bell both when food appeared and when it did not. (Pavlov 1927).

(3) Interocular generalisation. A conditioned response acquired using one eye is performed equally well using the other eye. Only if various parts of the brain are severed or removed is this power of generalisation lost. (Bibliography in Sperry, Myers and Shrier, 1960).

(4) "Transposition". This is the generalisation of the learned association to a slightly different though parallel situation. (e.g. Köhler 1918).

(5) Delayed, simultaneous and backwards conditioning. The two stimuli to be associated may be presented either simultaneously, or with the unconditioned stimulus (usually either reward or punishment) coming slightly before or after the conditioned stimulus. The situation in which the unconditioned stimulus is delayed about .5 sec has been traditionally held to give superior conditioning. (Pavlov 1929, Kimble 1961, Beecroft 1966). There is some uncertainty as to whether simultaneous presentation of the two stimuli yields a conditioned response or not. Beecroft's assessment that "though there is some evidence to suggest that weak associations are formed on a backward conditioning schedule, there is none which indicates that strictly

simultaneous conditioning takes place" is tempered by Rescorla's (1972) judgement that "there is surprisingly little data to force the conclusion that simultaneous conditioning does not occur".

(6) The "potentiation of habituation". This is the relearning with progressively greater rapidity of things already learned but in the interim forgotten.

(7) The remarkable resistance of conditioned responses to ordinary forgetting (as distinct from extinction). Responses have been elicited from animals when months and even years have elapsed since training. (e.g. list of papers in Hilgard and Marquis 1961, p.281).

(8) "Extinction": the undoing of an association by repeatedly presenting one part of the stimulus-pair without the other.

(9) "Spontaneous recovery": the reappearance after a time (e.g. 50 min, Ellson 1938) of the original conditioned response. This often occurs after a conditioned response has been "extinguished".

(10) "Disinhibition" (also called "dishabituation" or "the inhibition of inhibition") is the sudden increase in strength of a conditioned response (which may have been dying away or "extinguished") upon presentation of a different novel stimulus together with the unconditioned stimulus. This feature has been described as being "as ubiquitous as habituation" and "perhaps the most important method of distinguishing between habituation and 'fatigue'" (Thompson and Spenser 1966).

(11) A decreased rate of forgetting in sleep and darkness. This has been reported in studies as diverse as the remembering of nonsense syllables by humans, of visual discriminations by rats and fishes, and of shock avoidance by cockroaches (Van Ormer 1932, Thompson and Bryant 1955, Dücker and Rensch 1968, Minami and Dallenbach 1946).

The conclusion has been that a somewhat less rapid obliteration of memories occurs in darkness than occurs when further experience of a similar type follows the learning session (Thompson 1957, Minami and Dallenbach 1946). That the processes involved are not necessarily mental is suggested by cockroaches' acquisition and retention of 100% successful performance even when headless (Horridge 1962).