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AN INVESTIGATION OF SOME FACTORS AFFECTING THE VARIABILITY OF THE MCCOLLOUGH EFFECT

by

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Dedication:

To my parents, John and Cynthia Lund

ABSTRACT

A series of experiments are reported which have attempted to isolate some factors causing inter and intrasubject variability of the McCollough effect. A number of such factors were found.

1. The initial strength of the OCCA is strongly influenced by sleep duration. Reduction of up to one third of a normal nights sleep caused a marked decrease in the aftereffect strength. Sleep periods of under a third of normal were found to have no further effect. Decay rates were not affected by prior sleep duration.
2. Both the strength and decay of the McCollough effect undergo diurnal changes late in the evening. These changes were linked with the sleep cycle and evidence is presented indicating that the effect of the time of day upon the initial strength may be linked with the effect of sleep duration.
3. Some visual defects result in abnormalities of binocular, dichoptic and transferred McCollough effects.
4. Different visual stimuli presented after induction cause large variations in the rate of decay of the OCCA. Greatest decay was caused by those stimuli with identical characteristics to those of the induction stimuli.
5. Variation in the visual stimulation presented before induction strongly influences the initial strength of the aftereffect but does not affect subsequent decay rates. Chromatic fields of identical colours as the induction stimuli, and gratings of orientations of not more than 20 from those of the induction stimuli cause a large reduction in the strength of the OCCA.

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CHAPTER 1. INTRODUCTION

Of the many findings of visual psychophysics in recent years some of the most interesting have been the family of aftereffects which are contingent upon one or several parameters of visual stimulation suggesting that some elements (colour, form and motion for instance) are processed together to some extent. The aftereffects have attracted attention from both psychophysicists and neurophysiologists.

It had been postulated for some years before these discoveries that the visual system may have functional sub-systems for the processing of such elements as contours, orientation and colour (Hebb, 1949). Neurophysiological evidence for these feature extraction processes came from the work of Hubel and Wiesel (1959). They found neurones in the visual cortex of the cat which were excited by certain specific stimuli such as contrast bars, orientation, direction of movement, and length. One of the major questions when considering contingent aftereffects has been whether they represent evidence for mechanisms which respond selectively to specific combinations of visual features or evidence of associations between quite independent mechanisms.

One of the main groups of contingent aftereffects are the pattern contingent colour aftereffects. Neurophysiolgical evidence has been used to support both the view that pattern and colour are processed independently and the view that pattern and colour are processed together. For example, Yund, deValois and Hepler (1973) have found cells that respond selectively to specific form whether the form is represented by luminance gradients or colour gradients (the cells respond to colour but do not convey information about it). On the other hand, cells have been found in the monkey striate cortex which respond to specific colour and pattern combinations (Michael, 1978). The many psychophysical experiments concerned with pattern contingent upon colour will be reviewed later. To set both the historical and theoretical backgrounds it is worthwhile to consider two reports in detail: that of Gibson (1933), concerned with 'phantom fringes'; and McCollough (1965), concerned with the aftereffects which became known as the McCollough effect.

1.2. Phantom Fringes

Gibson (1933) noticed that the bluish and yellowish colour fringes, seen along edges while wearing prisms, decreased if they were worn for a long period (3 days) and that when the prisms were removed complementary coloured 'phantom fringes' were seen along edges for several hours. These phantom fringes are the first reported colour aftereffects contingent on form, the colour being selective to the direction of the edge contrast. The aftereffects were seen on vertical and oblique edges but not on horizontal edges. They were shown to be caused by a neural mechanism by Kohler (1951), who found that the phantom fringes could be seen in monochromatic sodium light.

The cells found in the cat visual cortex sensitive to the polarity and orientation of a light/dark border (Hubel and Wiesel, 1962), led McCollough to reason that the phantom fringes could be explained by the adaptation of separate edge-detector systems which are orientation specific, one system adapting to yellow and the other to blue. She further reasoned that if the edge-detectors were senstive to orientation it should be possible to adapt edge-detector mechanisms of differing orientations.

1.3. The McCollough Effect

McCollough (1965) reported an experiment during which she requested her subjects to inspect, without fixation, a screen on which horizontal blue and black gratings alternated with vertical orange and black gratings every few seconds. Subjects with normal colour vision were exposed to this alternation for 2 to 4 minutes. On viewing horizontal and verical black and white test gratings, they reported complementary hues to those originally paired with either orientation (an orange hue on horizontal gratings and a blue hue on vertical gratings).

In the 16 years since the original report there has been considerable interest in this, the McCollough effect, and other contingent aftereffects which have been discovered since. However, much of the subsequent literature has been concerned with the features of the effect which were found by McCollough.

One of the most striking aspects of the effect was the strong relationship of the orientation and induction and test gratings. Rotation of the test pattern (a horizontal grating beside a vertical grating) or rotation of the head through 90° caused the aftereffects to be seen on a different part of the test pattern.

Rotation through 45° (so that both gratings were at oblique angles) caused the disappearance of the hues. The aftereffects could be seen, after longer adaptation periods, on patterns of concentric circles, spirals or radiating lines but the hues were only apparent where the lines were predominantly horizontal or vertical.

There was evidence that the aftereffect was not an ordinary afterimage. The adaptation stimulus was not an intense one nor was it fixated. As the subjects moved their gaze about the test pattern, the aftereffect did not move but remained stationary on the test surface. The aftereffects could be seen on gratings rather than on a white test surface, unlike ordinary chromatic afterimages which are best seen on a plain white surface. The aftereffects were seen after repeated exposure to comlementary colours presented with gratings, but alternation of orange and blue fields alone produced no reports of afterimages.

Another feature considered by McCollough was the interocular transfer of the effect. The subjects viewed alternating orange-vertical and blue-horizontal with the right eye with the left covered, and then the left eye viewed the opposite colour and orientation pairing with the right eye covered. On testing, reports of hues were consistently reversed for each eye. McCollough concluded that the aftereffect does not transfer interocularly.

It was found that, like phantom fringes, the aftereffect could be seen in 'nearly monochromatic light' (using narrow-band pass filters). Hues of the aftereffect remained orange and blue in predominantly green, yellow and orange lights.

Finally, McCollough found that the aftereffect was very slow in fading. The effects persisted for an hour or more even after a brief exposure (2 to 4 minutes). McCollough inferred several things from her results: firstly, that they indicate colour adaptation of edge-detector mechanisms in the human visual system; secondly, that the mechanisms respond with decreased sentivity to those wavelengths with which they have been most strongly stimulated.

1.4. Variability of the McCollough Effect

One aspect which has perplexed investigators of contingent aftereffects is the enormous variability that is found between subjects and between the results obtained from the same subject on different occasions. Evidence of intersubject variability can be found in many reports (for example, McCollough, 1965 or MacKay and MacKay, 1975b). When subjects are used for a number of runs on different occasions it has been observed that large intrasubject variability also exists (Drs. V. MacKay and K. Bradshaw, personal communication).

It is apparent, when studying the numerous reports of aftereffects, that there is some variation in the results obtained by different investigators using apparently similar conditions. Some reports seem to contradict others (compare for example: Over, Long and Lovegrove, 1973 and MacKay and MacKay, 1973a). The major concern of this thesis is to identify some of the factors which can account for the variability of the McCollough effect.

CHAPTER 2. PARAMETERS KNOWN TO AFFECT THE PATTERN CONTINGENT AFTEREFFECTS

Many parameters of the McCollough effect have been manipulated, both in the adaptation and test phases, to determine its underlying cause. Much of the research stimulated by McCollough's report, has investigated her suggestion that the effect is evidence of adaptation of edge-detector mechanisms and has attempted to link features of the aftereffect with known physiological characteristics of the visual system.

2.1. Orientation

The finding that the orientation of the test grating is a crucial parameter in pattern contingent chromatic aftereffects (McCollough, 1965), has led to a number of reports which have used orientation as the dependent variable.

Most neurones studied in both the cat and monkey visual cortex show a high degree of orientation specificity. Simple and complex cell types respond optimally for a particular orientation of contour, the response falling off from this optimum. Most cells have an angular specificity of 10-15° in the cat and 5-10° in the monkey (Hubel and Wiesel 1962, 1968; Campbell, Cleland, Cooper and Enroth-Cugell, 1968). With reference to these data, Fidell (1970) reasoned that the McCollough effect may depend on the excitation of different populations of neurones in the human visual system, and that adapting the gratings whose angular separation is 90° should maximally excite the different populations. Her experiments showed that when adaptation gratings were at 90° to each other, but varying in absolute orientation, the aftereffects did not appear to vary in strength. When the angular separation was varied to 45° and 22°, however, the reports became less frequent. At 11° of separation, which presumably would stimulate the same population of neurones, reports of any aftereffect were very rare. Fidell considered her results to be consistent with an edge-detector interpretation of the effect.

It has been shown that it is possible to produce a contingent aftereffect with only one adaptation grating and that complementary hues are still induced on orthogonal test fields (Stromeyer, 1969). The hues could be 'neutralized' by rotating the adaptation grating through 90°. This raised the question of whether the orthogonal orientations are coupled to colours in an opponent fashion (as Murch, 1972 suggests) or whether gratings of orientations differing by some minimum angle are chromatically independent and would develop independent aftereffects. Data favouring the latter explanation, presented by MacKay and MacKay (1977a), showed that it is possible to generate an aftereffect to one, or to several, orientations simultaneously. They found that the aftereffect, generated by adapting to a single grating, has a bell shaped distribution. As the angle of the test field was rotated either way from the angle of the adaptation grating, the aftereffect fell to half value at about 25° difference and was maximum at the same orientation. When the adaptation gratings were presented at several orientations, the resulting aftereffect was shown to have an angular distribution which was the algebraic sum of those of each grating separately. It was possible to associate the same colour with two orthogonal orientations without any cancellation. MacKay and MacKay also found that the multiple aftereffects could be induced for at least 8 orientations at once and each showed an independent time course of decay (see section 2.8.).

Like Fidell (1970), MacKay and MacKay found that with separations of 15° between the orientation of the adaptation gratings, the aftereffects are barely significant. However, Stromeyer (1974) observed that the aftereffects can be induced with adaptation gratings separated by only 12°, if the test patterns are separated by a considerably greater orientation.

2.2. Spatial Frequency

The importance of the spatial frequency of the adaptation and test grating to the McCollough effect, was first shown by Teft and Clark (1968). Using the strong orientation dependency of the effect, they found that the degree of rotation of the test field from that of the adaptation grating, before the aftereffect disappeared, was decreased as the spatial frequency of the test grating departed from that used during adaptation.

It has been demonstrated that the aftereffects are strongest when the test gratings have the same spatial frequency as the adaptation gratings (Stromeyer, 1972a). Using adaptation gratings and test gratings ranging from 1 to 20 cycles per degree, Stromeyer found that the effects became progressively weaker on test gratings with a higher or lower spatial frequency than the adaptation gratings. The effects, however, were still detectable 2 or 3 octaves either side. He also demonstrated that the complementary aftereffects cannot be induced by patterns of the same orientation and different colours, unless the spatial frequencies differ. The effects have been shown to be difficult to produce with adaptation gratings which have only a half-octave separation, but are readily produced using gratings that are separated in spatial frequency by one or more octaves (Lovegrove and Over, 1972). In addition, Lovegrove and Over found that one grating must have a spatial frequency greater than 3 cycles per degree. Using a 3.3 cycle per degree grating of either red or green, with gratings of the same orientation and the complementary colour, Breitmeyer and Cooper (1972) found that the number of reports of the aftereffect increased as the difference between the spatial frequencies increased. The reports ranged from 0, when the spatial frequencies were the same, to 100% when they differed by 2 octaves. These reports are consistent with neurophysiological findings that some cortical and geniculate cells are sensitive to spatial frequency (Campbell et al, 1969). Units in this study responded to gratings up to 1 octave from their optimum frequency.

It has been reported that after adapting to two horizontal gratings of different spatial frequencies and colours, aftereffects could be seen on both horizontal and vertical gratings of the appropriate spatial frequencies (Leppmann, 1973). The effects were strongest on the portions of a variable frequency test grid which corresponded to the adaptation frequencies. Leppmann suggested that his results may indicate mechanisms which are spatially tuned but not orientation selective.

Attempts have been made to isolate the relative influence of spatial frequency, black bar width, and light bar width. Using vertical gratings of 4.5 and 9 cycles per degree, with red and green fields and vertical gratings with black and white bar width ratios of 1:3, 3:1, 1:1, Harris (1971) concluded that the aftereffects were dependent on spatial frequency rather than bar width. In contrast, Uhlarik and Osgood (1974) found that the afterffects were strongest when the black bars of the adapting and test gratings were similar in width. The white bar width and the spatial frequency had less effect.

2.3. Pattern aftereffects contingent on colour

A number of people have reported 'reverse' McCollough effects which are pattern aftereffects contingent on colour, and have demonstrated the orientational and spatial frequency properties of these effects.

After viewing red and green gratings tilted 10° clockwise or anticlockwise from vertical, subjects reported that vertical lines, when coloured red or green, appear tilted in the direction opposite to that of the adaptation pattern with the same colour (Held and Shattuck, 1971). The direction of the tilt aftereffect was dependent on colour. It was demonstrated that the amount of tilt varied as the angle between the adaptation and test gratings was changed. Using vertical test gratings, but increasing the angle of the adaptation gratings from, 0° to 75°, the magnitude of the aftereffect increased rapidly to a peak between 10° and 15°, then dropped close to zero at about 40°.

A spatial frequency shift effect, that is contingent on colour, has also been reported (Virsu and Haapasalo, 1973). After adapting to a red 7 cycle per degree grating, alternating with a green 2.5 cycle per degree grating, subjects viewed a test grating of 4 cycles per degree split into green and red coloured halves, above and below a fixation mark. The spatial frequency of the two halves then appeared different. The half coloured red appeared to be a lower frequency and the half coloured green appeared to be a higher frequency.

2.4. Luminance and Contrast

The luminance of adaptation and test patterns can be considered in two ways. One can consider the luminance of the whole pattern, or the luminance of the individual components (the contrast) of the patterns.

(a) Luminance

It has been noted that the phantom fringes, observed after wearing prisms, are most vivid in dim illumination but are not visible at scotopic levels of illumination (Kohler 1951). Hay, Pick and Rosser (1963) also observed that phantom fringes were not visible in scotopic illumination (below 10^{-3} mlm) but concluded that the strength is unaffected by different photopic levels of the test patterns. The McCollough effect, however, is visible at both scotopic and photopic levels (Stromeyer 1974). Stromeyer found that after adapting to broad gratings at photopic levels, subjects reported aftereffects even when the luminance level of the test grating was reduced to below 10^{-4} mlm. In an experiment varying both the luminance of the test and adaptation stimuli, White (1976) showed that the aftereffect strength increased with higher luminance of the adaptation stimuli and with lower luminance of the test stimuli. Others have also noted that McCollough effects tend to be seen best on dim test gratings (Skowbo, Gentry, Timney and Morant, 1974). The range of adaptation and test stimuli luminances used in different experiments have varied widely.

(b) Contrast

Both phantom fringes and the McCollough effect require luminance contrast in both the adaptation and test stimuli, before aftereffects are produced. Phantom fringes can only be seen on edges that have a luminance contrast. Edges that are defined by colour differences alone have been shown to be ineffective (Kohler, 1951). Hay et al (1963) showed that the phantom fringes became more vivid as the contrast of the test pattern was increased. The McCollough effect is obtained only by using adapting patterns which contain luminance contrast (Harris and Barkow, 1969). Both black-coloured and white-coloured gratings produce aftereffects, but the black-coloured gratings were more effective. Mikaelian (1980), using similar conditions, has obtained similar results. The results of Stromeyer and Dawson (1978) show that no aftereffects are produced with coloured gratings which lack luminance contrast. They observed that, after adapting to low spatial frequency gratings of either coloured and black gratings or coloured and white gratings that fell approximately in one retinal position, aftereffects were only seen clearly on test gratings when the patterns were positioned on the retina so that the local luminance contrast of the adapting and test patterns matched.

2.5. Hue

Hue has been utilized as an independent parameter in very few of the studies of the McCollough effect. McCollough (1965) used orange and blue adaptation fields but reported that 'the choice of filters is not critical: distinguishable, though unsaturated, aftereffects can be obtained with most pairs of filters which clearly differ in their transmission characteristics'. In most studies adaptation colours have been red and green. Using alternating vertical and horizontal adaptation gratings with red, yellow, green or blue filters, Hajos (1968) found that the aftereffects produced on test gratings were often named as red or green but very few yellow and blue effects were reported. In another study in which colour was the independent variable, Stromeyer (1969) used a variety of colours presented with only one adapting grating (the colours were not paired) and a test pattern which was also a grating of one orientation. He found that the aftereffects produced by red and blue-green colours were the strongest and were green and pink respectively. Adapting colours near to blue occasionally produced weak yellowish aftereffects, but there was little evidence that yellow adapting colours produced blue aftereffects. In a later report Stromeyer (1972a) found that the strength of the aftereffect for a given adaptation colour seemed to vary with the spatial frequency of the adaptation gratings. Aftereffects following adaptation to blue and orange could be produced if these colours were presented with the appropriate spatial frequency grating.

2.6. Monocularity and Binocularity

One particularly interesting aspect of McCollough's report was that different aftereffects could be induced succesively and retained independently in either eye. She concluded that the effects failed to show interocular transfer. Visual aftereffects not selective to colour have, however, been shown to transfer. For example, the tilt aftereffect (Campbell and Maffei, 1971) and the changes in contrast thresholds induced by adapting to a grating (Blakemore and Campbell, 1969), both transfer and the apparent spatial frequency shift (Blakemore, Nachmais and Sutton, 1970) transfers partially.

Most aftereffects contingent on colour do not appear to transfer interocularly. Opposite sets of phantom fringes can be induced in separate eyes and are seen only with the adapted eye (Hajos and Ritter, 1965). Many investigators have noted that on adapting one eye, no McCollough effect can be seen with the unstimulated eye (Murch 1972, Stromeyer, Lange and Ganz,1973 and MacKay and MacKay, 1975b). The apparent spatial frequency shift can be used to modify the spatial frequency, which may in turn change the colour of the McCollough effect. The spatial frequency shift transfers to the unadapted eye but no colour change is seen (Stromeyer, 1972a). Colour aftereffects contingent on the direction of a spiral do not transfer to an unadapted eye (Stromeyer and Mansfield, 1970) nor do motion aftereffects contingent on colour (Mayhew and Anstis, 1972) In both cases opposite effects can be induced simultaneously in separate eyes. Shattuck and Held (1975) have shown that colour contingent tilt aftereffects do not transfer interocularly and opposite effects generated simultaneously in either eye do not cancel each other.

Although these reports suggest that colour contingent aftereffects are largely monocular, more recent studies have shown some degree of interaction between eyes. The McCollough effect can be induced dichoptically if one eye is exposed to alternating orthogonal gratings, while the other is simultaneously exposed to alternating red and green homogeneous fields, one orientation being paired with one colour (MacKay and MacKay 1973a, 1975b). Colour aftereffects are produced in both eyes but the aftereffects produced in either eye are different. The eye exposed to colour only has hues which are complementary to those originally paired during adaptation and the eye exposed only to pattern has hues the same as originally paired (these MacKay and MacKay called 'anomalous' McCollough effects). The aftereffects in both eyes showed a similar time course of decay to normal McCollough effects of the same initial strength, but their strength was only 0.1 to 0.3 times the strength of a normal McCollough effect produced with the same period of adaptation. Using similar experimental conditions Over, Long and Lovegrove (1973) found no dichoptic interaction of the McCollough effect.

Colour contingent motion aftereffects can be induced by dichoptic stimulation, but when one eye is exposed to colour and the other eye is simultaneously exposed to a moving achromatic spiral, the aftereffect is seen only in the eye exposed to colour (Murch, 1974). Potts and Harris (1979) report similar results, again finding no 'positive' aftereffect in the eye exposed to movement alone. The tilt aftereffect, when induced in coloured light, has been shown to be larger when the test stimulus is viewed in the same, rather than a different, coloured light (Held and Shattuck, 1971). However, this colour specificity is not seen when the colour and the test gratings are viewed dichoptically (Broerse, Over and Lovegrove, 1975).

Although Mayhew and Anstis (1972) reported no transfer in a colour contingent motion aftereffect, it has been observed that on adapting one eye only, the usual negative colour contingent aftereffects are seen in the adapted eye and opposite 'positive' aftereffects are sometimes seen in the unadapted eye (Favreau, 1978). A similar result has been reported when studying the McCollough effect (Mikaelian, 1975). The normal negative colour contingent orientation aftereffects are seen in the adapted eye and positive aftereffects are seen in the unadapted eye, but only after binocular viewing of the test pattern; this Mikaelian terms interocular generalisation of the McCollough effect. MacKay (1978) repeated the procedure used by Mikaelian and could find no such interocular generalisation but reported very weak normal negative aftereffects in the unexposed eye which were below 10% of the strength of the adapted eye. They were not noticeably increased by having a light or dark input to the unadapted eye, or by ensuring that either eye's imput was suppressed during exposure and-or testing. In a study of binocular interactions during adaptation of the McCollough effect, White, Petry, Riggs and Miller (1978) found that interocular transfer was facilitated if one eye received a full McCollough stimulus while the other eye viewed simultaneous homochromatic stimulation. When the homochromatic stimultion was the same colour as the McCollough stimulus the aftereffect in the eye presented with colour was, as in the dichoptic experiments of MacKay and MacKay (1973a, 1975b), complementary in hue to the original colour-orientation pairing. When the homochromatic stimulation was a different colour the hues were the same as the original pairing (they were, however, transient and did not last as long as the normal McCollough effect). MacKay (1978) in a similar series of experiments, found no transfer when the colours, presented to the two eyes during adaptation, were different. She further reports that achromatic gratings presented to one eye also facilitate transfer if the other eye receives a full McCollough stimulus. When achromatic gratings were the same orientation during adaptation, the aftereffects were the same hue as the original pairing (anomalous McCollough effects), but when the orientations were orthogonal during adaptation, normal complementary hues were seen.

The McCollough effect has been shown to have a binocular component (Vidyasager, 1976). Vidyasager used an adaptation sequence of three parts, binocular and monocular in each eye, of equal durations, with short dark intervals between each. If no binocular component was involved, no McCollough effect would have been produced either binocularly or monocularly as the binocular stimuli were the reverse set of colour and orientation pairings to the monocular stimuli. He reported that after thirty minutes of a repeated sequence of red vertical, binocular; blue vertical, right eye; red horizontal, right eye; blue horizontal, binocular; red horizontal, left eye; blue vertical, left eye, a test pattern viewed binocularly appeared bluish with vertical gratings and pinkish with horizontal gratings. When viewed monocularly, aftereffects of the reversed polarity were seen. These aftereffects, though small, showed a comparable time course of decay to ordinary McCollough effects. Further evidence of a binocular component is provided by the observation that, after binocular adaptation, the McCollough effects seen binocularly are larger than those seen monocularly (MacKay, 1978 and White et al, 1978). MacKay (1978) also reports that if the two eyes are presented with the same McCollough stimuli, but not simultaneously, the aftereffects seen binocularly are considerably smaller (about 33%) than those seen monocularly. The size of the colour contingent tilt aftereffect has been found to be no different when the adapting stimuli are the same in both eyes, from when they are the reversed pairing in either eye, showing no interaction between the eyes (Kavadellas and Held, 1977).

2.7. Retinal Specificity

Several studies have demonstrated that McCollough effects are confined to specific adapted portions of the retina. Opposite aftereffects can be produced in adjacent retinal areas so that, for example, horizontal lines on one part of the retina might appear green but in a different area could appear red (Harris, 1969). After fixating an alternating pair of colour orientation gratings, Stromeyer (1972b) showed that the aftereffect hues which his subjects judged to be most saturated, occurred when the test grating approximately coincided with the adapted area and were less saturated as the overlap was reduced. If the test grating was moved as little as 0.5° away from the adapted area, it appeared colourless. Retinal specificity was perhaps most strikingly demonstrated by Stromeyer and Dawson (1978) who used two sets of vertical, 2 cycles per degree gratings of different hues for their adaptation stimuli. These were presented sequentially in counter-retinal positions, the coloured bars of one grating filling the retinal area occupied by the black bars of the other grating. A vertical test grating then appears pink when placed in a position occupied by the black bars of a green grating and green when placed in the position occupied by the red grating.

The importance of eye movements to the McCollough effect has been studied by Piggins and Leppmann (1973) using a contact lens technique to investigate the aftereffects, after adapting with stabilised patterns. They found that no hues were reported when the test stimuli were either stabilised or freely scanned. However, subjects consistently reported weak aftereffects after adaptation to sine wave gratings presented for only 9msecs. every second (Stromeyer, 1974b). Using such stimuli, eye movements greater than 1' of arc are highly unlikely during fixation. Stromeyer further notes that subjects report aftereffects when square wave gratings are presented for only 60μsecs.

2.8. Time Course of the Aftereffects

One of the most noticeable features of form colour aftereffects is the length of time they take to disappear. Phantom fringes are visible for several hours after wearing prisms for a number of days (Gibson, 1933). Kohler (1951) noted that in dim illumination weak aftereffects could be seen for several days after 50 days of adaptation. Colour motion contingent aftereffects last up to 27 hours following 3 - 5 hours of adaptation (Hepler, 1968). Similarly, Stromeyer and Mansfield (1970) found that after adapting to moving colour gratings for 20 minutes, aftereffects were commonly seen for a day or more and some were found to last up to 6 weeks.

The persistence of the McCollough effect was first noted by McCollough (1965) who found aftereffects lasting an hour or more following only 2 to 4 minutes adaptation. After 2 hours of adaptation, Stromeyer (1971), observed that the aftereffects were visible for 2 weeks. He also reported that, on increasing the adaptation time, the 'saturation' of the aftereffects appeared to strengthen for up to about 90 minutes of adaptation. In a study of the build up and the decay of the McCollough effect Riggs, White and Eimas (1974) found that the strength of the aftereffects, as measured by a cancellation technique, increased with lengthened adaptation times up to 150 minutes. Strong aftereffects lasted for more than 7 days. They also found that the aftereffects followed a characteristic time course of decay, with curves that were not quite straight either on log-log or linear-log coordinates. MacKay and MacKay (1973b, 1975a) have also studied the decay curves of the McCollough effect and found that they are approximately linear on log-log coordinates with a slope of -1/3.

The strength and the decay of the McCollough effect are affected not only by varying the total adaptation time, but also by varying the temporal parameters of the elements of the adaptation sequence (the 'on' and 'off' periods). Estimates of the strength of the effect were found to be proportional to the total light 'on' periods and affected by the length of the dark 'off' periods (Hajos, 1968). The length of the 'on' periods however, has no effect over the range of 0.5 to 4 secs. Bradshaw (1978) found that, although most decay curves are linear on log-log coordinates, certain sequences are more linear on linear-log coordinates. These differences were independent of the total adaptation time, and probably independent of the total cycle time and the 'on' 'off' ratio, but were strongly influenced by the 'on' interval alone. Short 'on' intervals (1s. or less) were associated with steeper decay curves which were more linear on linear-log coordinates. It was also found that the 'on' interval had a substantial influence on the strength of the aftereffect as it was increased to 1s, but had little influence beyond this. Like Riggs et al (1974), Bradshaw found that the strength increased as the adaptation period is increased.

The persistence of the McCollough effect has led to numerous reports on the effect of different stimuli, or lack of them, on the decay of the aftereffects. Prolonged viewing of the achromatic test gratings has been shown to cause the aftereffects to fade (Stromeyer, 1972a). This observation has been repeated by Skowbo, Gentry, Timney and Morant (1974) and Skowbo and Clynes (1977). Greater exposure leads to a greater fading and less recovery following a rest period (Skowbo and Clynes, 1977). High luminance gratings, presented after or before adaptation, interfere with the aftereffect more than low luminance gratings (Skowbo, 1979). In a study of the persistence of the aftereffect, Jones and Holding (1975) reported that test measurements, using achromatic gratings, permanently reduce the effect but little decay occurs over an 8 day period, following adaptation, if no test patterns are viewed. Skowbo et al (1974) found that, although achromatic gratings produce a fast decay, homogeneous chromatic fields, natural visual stimulation and complete darkness had a similar much less rapid decay. However, MacKay and MacKay (1974a, 1975a) have found that no decay at all occurs if an eye is kept in complete darkness after adaptation, even though the aftereffect in an eye exposed for the equivalent period, to either diffuse light or the natural environment, decays substantially. An eye kept in darkness retains the McCollough effect until it too is exposed and then it decays in exactly the same manner as the eye which was originally exposed. MacKay and MacKay (1975a, 1977b) also report that, when studying the decay of the McCollough effect for several days, the effects were often higher following sleep than the effects measured the night before. They suggested that these results indicate that the McCollough effect is not caused by fatigue of colour coded edge-detector mechanisms, as originally proposed (McCollough, 1965), but by something like associative habituation of synaptic couplings, since decay only occurred when some stimuli or interference occurred within the eye.

2.9. Further factors affecting the variability of the McCollough Effect

Although many of the factors which influence the McCollough effect have been investigated, numerous inconsistencies exist between reports from different investigators. Detailed inspection of various reports, and my own preliminary investigations, have revealed that, even when the known factors are kept constant, considerable intrasubject and intersubject variability still exists.

Recent evidence has shown that the McCollough effect is probably not due to selective adaption of colour sensitive edge-detector neurones, but to some associative (possibly synaptic) habituation (MacKay and MacKay, 1974a, 1977b). It is possible that many factors of normal life may disrupt the linking or breaking of these associations. Such elements could include hormonal levels, different food intakes, different drug levels and varied visual stimulation. A number of reports have indicated how the McCollough effect can be affected by these factors. Recent evidence has shown that some drugs may influence the McCollough effect (Shute, 1978, 1979; Amure, 1978, 1979). Shute has shown that agents affecting cholinergic function (hyoscine, ethopopazine, mecamyamine), tranquillisers (benzodiazepines) and agents influencing the catecholamine system (premoline) all reduce the decay and raise the initial strength of the McCollough effect. Caffeine reduces the initial strength and produces faster decay of the effect (Shute, 1978; Amure, 1979); nicotine reduces the decay of the effect (Amure, 1978). Bradshaw (1978) found no effect using a number of barbiturates or an amphetamine. Dr. V. MacKay (personal communication) found that the McCollough effect varied when induced at different times of the day. This may indicate the influence of diurnal changes in hormonal levels. When a period of sleep interrupts the measurement of decay the McCollough effect is larger after sleep than the effect measured immediately before (MacKay and MacKay, 1977b). This may also reflect some diurnal change.

A number of reports have demonstrated the influence of different visual stimulation on the McCollough effect, after adaptation (see section 2.8.), but little has been reported about the effect of pre-adaptation visual stimulation. Skowbo (1979) has demonstrated that high luminance gratings, presented before adaptation, reduce the initial strength of the McCollough effect. Visual stimulation before adaptation may be an important factor in the variability of the effect, as it may vary on different days and between subjects.

The research reported in this thesis has attempted to isolate some of the factors responsible for the variability of the McCollough effect.

CHAPTER 3: EQUIPMENT AND EXPERIMENTAL PROCEDURE

3.1 Introduction

Members of the Department of Communication and Neuroscience had been researching into certain aspects of the McCollough effect for some time. The equipment available, with a few modifications, was adequate for all the experiments reported. Two pieces of equipment were used for the experiments; a tachistoscope for induction of the effect and a variable hue device for measuring both its pre- and post-induction strength. The tachistoscope was also used to present visual stimuli before or after induction (see Chapters 8 and 9).

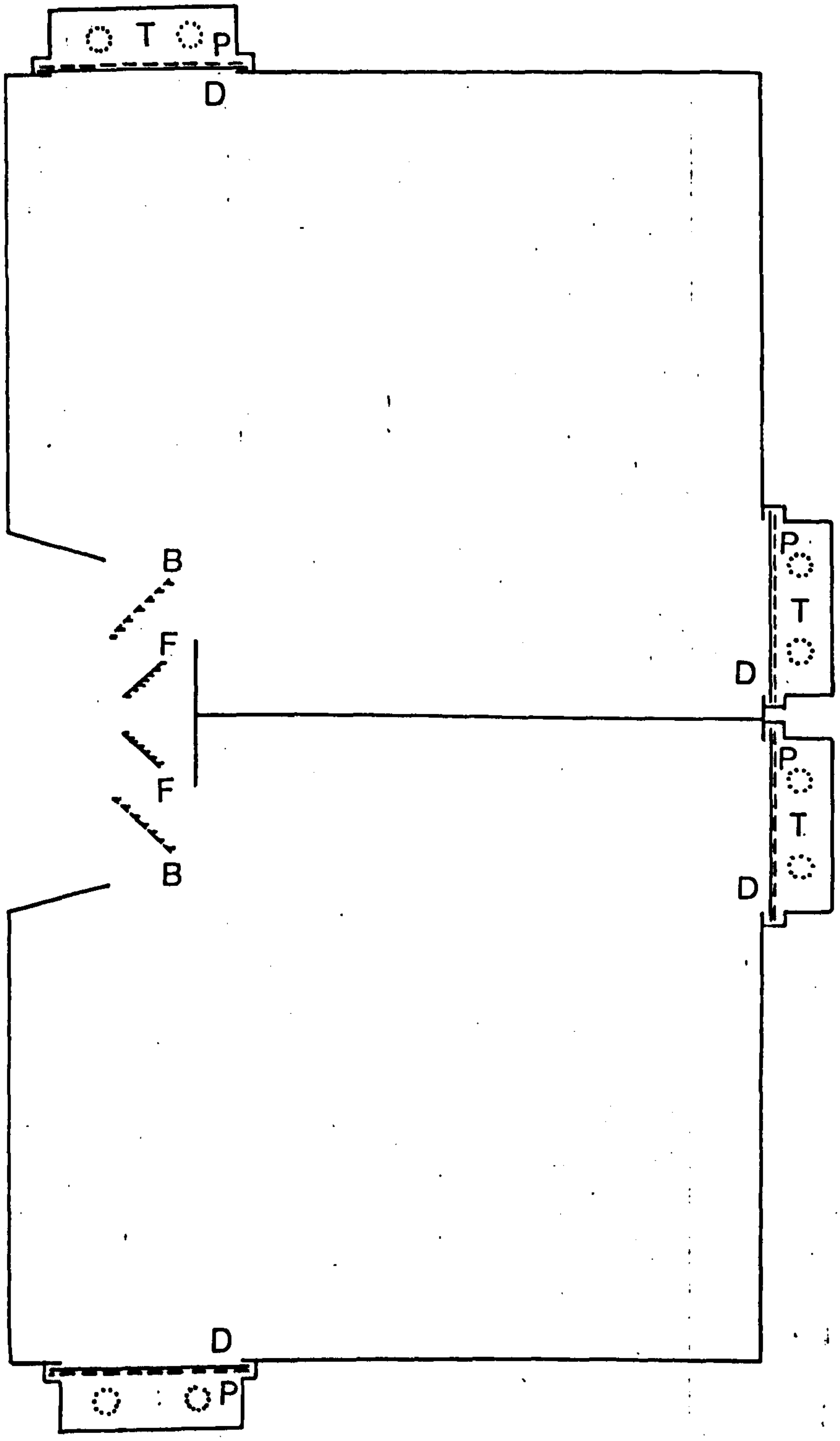
3.2 Induction of the McCollough Effect

The McCollough effect was induced using high contrast patterns with various colour filters presented by the tachistoscope to one or both eyes.

3.2.1. Tachistoscope

A four field tachistoscope (fig. 3.1.) was used to present the induction stimuli. In every experiment two alternating stimuli were presented for equal periods of time with a dark interval between. The length of the stimulus 'on' periods could be varied from 0.1 to 20 seconds by changing the duration of the square wave pulse provided to each field. Repeat accuracy was in the range of +0.5% to +2%. The dark, or 'off', periods could be varied by changing the duty cycle with a Wavetek Function Generator. The duty cycle was controlled by two outputs from the Wavetek which were 180° out of

Fig. 3.1. Tachistoscope (After Bradshaw 1978)



D, Perspex diffuser: P, Adaptation pattern and filter: B, Beam splitter: F, Front surface mirror: T, Fluorescent tube.

phase. Frequent checks of both the 'on' and 'off' periods were made using a light sensitive cell and a storage cathode ray tube. Each field was back-illuminated, during the 'on' period, by two fluorescent tubes (54vl 'Daylight'). A perspex 'milk-white' diffusion screen ensured uniform illumination of the entire field. Pattern frames, with a window 10.5cm. square (12 x 12° angular subtense at the eye), were used to locate the patterns accurately. Fixation circles, with a diameter of 1.75cm (2° angular subtense at the eye), were scratched into the surface of clear perspex sheets. These sheets were positioned in front of each field. Illumination of the edge of the perspex sheets with low voltage bulbs caused the fixation circles to glow. Metal slide guides were used to retain the tube boxes, the diffusing screen, the induction patterns and the clear screen.

Fields 1 and 2 were used to present alternating stimuli to the right eye and fields 3 and 4 presented stimuli to the left eye. Fields 1 and 3 were triggered simultaneously from output A of the Wavetek, and fields 2 and 4 were triggered simultaneously from output B. The stimuli to the two eyes were usually identical (i.e. fields 1 and 3 and fields 2 and 4 contained identical stimuli). The fields were optically superimposed by an arrangement of front-silvered mirrors and beam splitters. The front-silvered mirrors could be finely adjusted with screws to ensure that the fields were superimposed binocularly. The beam splitters could be rotated in the horizontal and vertical planes to superimpose the fields to each eye. The fixation circles of the four fields were superimposed. This arrangement helped binocular fixation in both the 'on' and 'off' periods. A central dividing screen, in the tachistoscope, restricted light scatter to either eye. Stimuli were presented monocularly by switching two fields off (either fields 1 and 3 or 2 and 4).

3.2.2. Patterns

The patterns used were square wave gratings of 2.85 cycles per degree presented at orthogonal oblique angles (+45 and -45 to the vertical). Most investigators in other laboratories have used horizontal and vertical gratings. Oblique gratings were used here for two reasons. Firstly, the man-made environment contains more high contrast vertical and horizontal edges than oblique ones. If such edges are coloured they can induce small McCollough effects either before an experiment or during decay. Non-coloured edges may also influence the McCollough effect as gratings presented before or after induction interfere with the effect (Skowbo 1979). These influences may result in scatter or bias. The use of oblique gratings does not eliminate the problem but does reduce it. Secondly, special sensitivities for horizontal and vertical orientations have been found in the human visual system (Campbell, Kulikowski and Levinson, 1966; Hirsch, Schneider and Vitiello, 1974). The horizontal and vertical sensitivities were not identical. Oblique gratings are therefore more balanced with respect to each other.

3.2.3. Colour Filters

In every experiment reported one induction pattern was projected through red (590-670nm) and the other through green (480-560nm) 'Cinemoid' filters (14 and 24 respectively). The patterns were matched for luminance by using two layers of red and three layers of green filter.

Many investigators have used 'Wratten' magenta and green filters (34a or 32 and 53 respectively) which are exact complements of each other. These filters, however, are band stop filters and the magenta transmits blue wavelengths. The 'Cinemoid' filters were preferred because they are fairly narrow band pass filters.

3.2.4. Luminance

The luminances of the coloured stripes of the gratings were matched at approximately 5mlm. The luminances of the dark stripes were approximately 0.2mlm.

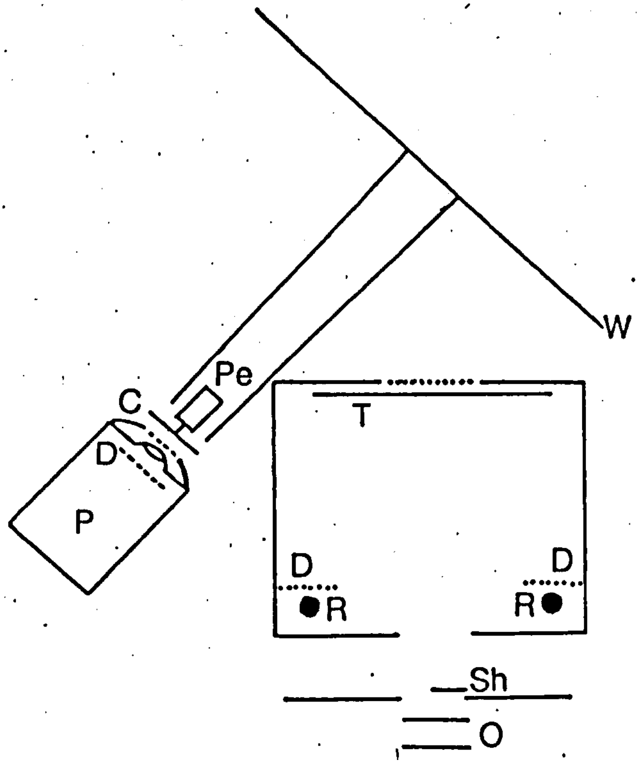
3.3. Measurement of the McCollough Effect

The presence or absence of the McCollough effect can be tested simply by providing an achromatic test pattern of appropriate spatial frequency and asking for a verbal report. The experiments reported in this thesis, however, required a quantitative measure of the strength of the effect. Verbal reports were recorded but a colour matching device was used to obtain, in arbitary units, an objective measure.

3.3.1. Apparatus

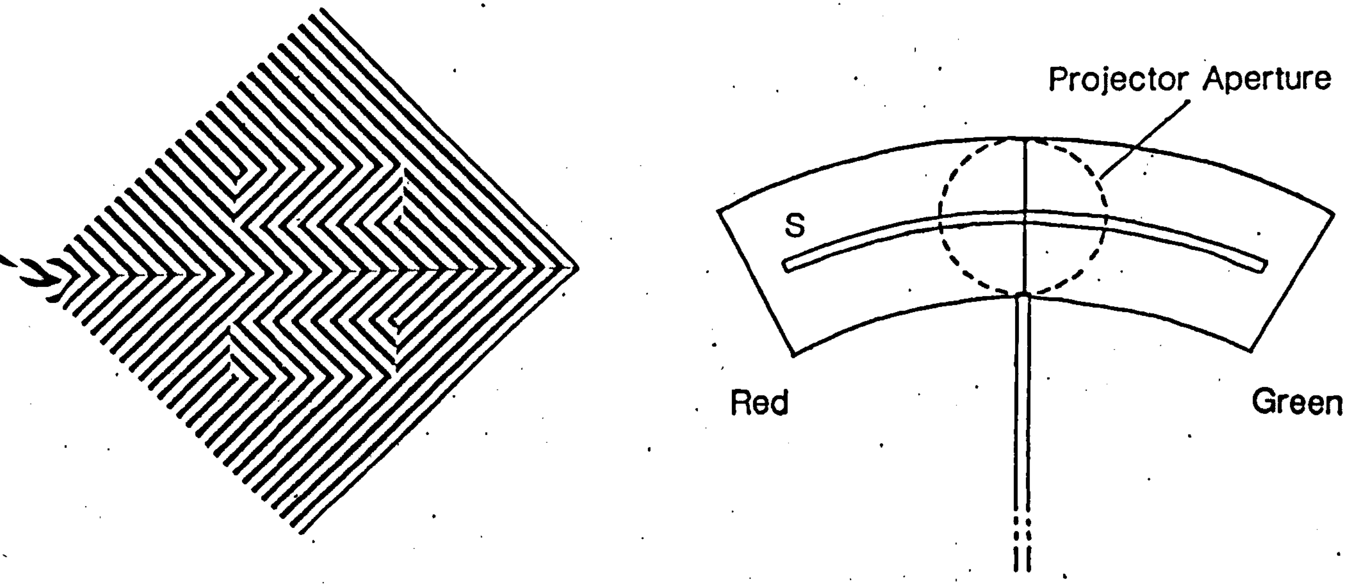
The apparatus used to record the strength of the effect (fig. 3.2a.) was a modified version of the equipment used by MacKay and MacKay (1973b, 1975b). The measurement of the effect was made by a 'match and null' technique (see Appendix A for a discussion of

Fig. 3.2



(a) Test Apparatus.

C, Moveable red and green filters: P, Projector: D, Diffusing paper: R, Ring tube: Sh, Shutter: O, Chin rest: Pe, Pen motor: T, Test pattern: W, White reflecting card.



(b) Test Pattern

(c) Adjustable Colour Filters

S, Slit in filter:

methods of measurement). The test pattern (fig. 3.2b.) consisted of two orthogonally orientated achromatic gratings positioned side by side, with a small translucent window in each half. The gratings of the windows were orthogonal to the surround gratings. The whole test pattern was 15cm × 15cm (10°30' angular subtense at the eye) and the windows were 6.5cm × 2.2cm (4°35' × 1°35' angular subtense at the eye). The gratings were 2.85 cycles per degree. The windows were illuminated from the rear by reflection from a 100W projector. The pattern was illuminated from the front by an annular fluorescent tube (Cryselo 'Warm White' 32W), which could be adjusted to match the windows. The luminance of the white stripes was 4mlm and that of the dark stripes 0.1mlm. The mean test luminance was thus lower than the mean luminance of the induction gratings. White (1976) has reported that the largest McCollough effects were seen using high luminance induction gratings and low luminance test gratings. The front illumination was slightly yellow to match the yellow produced by the red-green mix of the windows. The subjects were kept at a fixed distance from the test pattern by a chin rest. The test pattern could be presented binocularly or monocularly to either eye by means of a shutter which could cover either or neither eye. Red and green filters were positioned in front of the 100W projector lens (fig. 3.2c.). They were attached to a pen motor by an extension arm and could be moved over the aperture of the projector. The displacement of the red-green boundary and thus the ratio of red to green light being projected, provided the colour change of the apparatus. The light was projected onto a white card which reflected it to the back of the translucent windows of the test patterns. The colour was desaturated by a slit cut in the filters, which admitted a fixed amount of white light. A smooth knob controlled the input to the pen motor, so that little indication of its position was given to the subject. The shift circuit of the Y-axis of an X-Y chart recorder received a parallel input to the pen motor. The movement of the red-green boundary was thus linearly related to the movement of the marker pen of the recorder (see section 3.3.2c.). A switch arrangement moved the zero of the marker pen to one of three positions on the chart to allow the binocular, right eye and left eye records to be separated. The X-axis of the chart recorder allowed the McCollough effect to be measured as a function of time. The tests required the subject to match the colour of each window with its surround. A two way switch was used to drop the marker pen onto the chart. Moving the key one way caused the pen to drop and make a dash on the chart, while the reverse movement caused the pen to make a dot. The difference between the marks was linearly related to the displacement of the red-green boundary and represented the difference between the excess of red over green at one window and the excess of green over red light at the other window. This difference was taken as the measure of the McCollough effect at that time.

3.3.2. Calibration of the Apparatus

The linearity and sensitivity of the test apparatus was investigated using the following methods:

(a) Projector luminance

The red-green boundary was moved over the projector aperture, therefore it was necessary that the luminance of the aperture was uniform. Non-uniform luminance would lead to the colour and luminance of the test being confounded. The luminance was made as uniform as possible by using diffusing paper within the projector. It was measured at 1cm intervals across the aperture using a photometer, and did not vary significantly.

(b) Linear range of the filters

The red and green filters on the extension arm were arranged so that a full scale deflection of the potentiometer controlling the colour match just moved the boundary to either edge of the projector aperture. The slit in the filters admitted the same amount of white light over the whole range. The maximum range of the red-green boundary corresponded to a deflection of 8cm of the marker pen on the chart recorder. The McCollough effect observed were seldom more than 5cm. The surplus deflection was necessary as the measurements were often 'slewed', each adapting colour inducing a different effect (see section 3.7.3.). This slewing effect varied in magnitude and polarity between subjects.

(c) Chart recorder and pen motor relationship

The relationship between the pen motor and the chart recorder was investigated by measuring the displacement of the red-green boundary for each 1cm movement of the recorder pen. Each 1cm movement of the pen was found to correspond to equal displacements of the boundary. The relationship was therefore linear.

(d) Relationship between the test card colour and the colour match

The test equipment was used to study a large range of aftereffect strengths. It was necessary that the apparatus should be able to measure different strengths equally well. This ability was tested by studying the colour match of the windows in relation to the colour of the surround. Subjects first made a colour match of the upper and lower windows with their respective surrounds. This indicated any orientationally linked bias present. Only subjects with no initial bias were used. Red filters were then placed over the annular fluorescent tube which illuminated the test pattern. As the filters were added the surround became progressively more red and subjects made repeated colour matches until the tube was completely covered. The colour saturation of the test card was then greater than any observed aftereffect for any subject studied. Colour matches were also made as the filters were removed. The whole procedure was then repeated using green filters. The results are plotted in fig.3.3. and show a smooth curve. This shows that the equipment is equally sensitive throughout the range of the aftereffects measured.

(e) Time

The chart recorder plots could be read to 0.05 minutes with the paper speeds generally used.

3.4. Experimental procedure

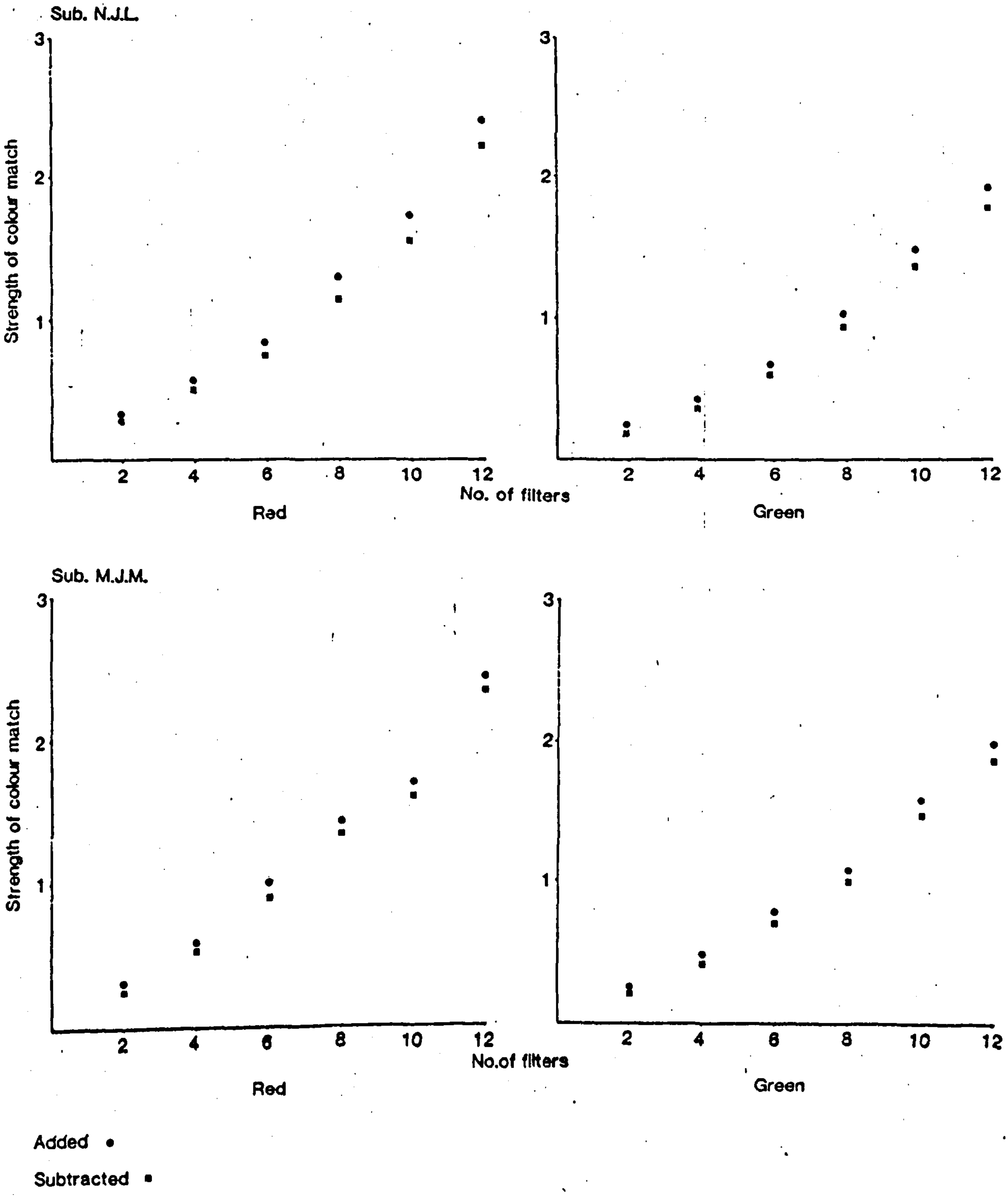
The experimental procedure normally consisted of three phases:

(1) a pre-induction test to check for any orientationally linked colour bias or residual aftereffect;

(2) an induction phase which consisted of a period of exposure to alternating orthogonally orientatated gratings of opponent colours;

(3) a post-induction phase during which the strength of the induced

Fig. 3.3.


Sub. N.J.L.
Strength of colour match
3
2
1
2
4
6
8
10
12
No. of filters
Red
Green
Sub. M.J.M.
Strength of colour match
No.of filters
Red
Green
Added ●
Subtracted ■

aftereffect was measured over a period of time.

Extra pre-induction tests were performed for the experiments reported in Chapter 8. The experiments reported in Chapter 9 required two or more periods of post-induction measurement.

3.4.1. Pre-induction Test

All experiments were conducted at a low level of room illumination.This level remained constant throughout the experiment. Before the pre-induction test took place the subject adjusted to this level while the procedure was explained. A chin rest ensured that the subject viewed the test pattern from a fixed distance of 72cm. The luminance of the surround was adjusted to match that of the windows while the colour bias was neutral. As the subject viewed the test pattern he was shown how to vary the colour of the windows with the smooth knob. It was explained that his task was to match the colour of the upper window with its surround and to press the key, connected to the pen of the X-Y chart recorder, away from him and then to match the colour of the lower window with its surround, pulling the key towards him. He was told that turning the knob too far one way would make the window too green and the other way too red. The subject was requested to make the match carefully but rapidly by deciding on the best position if the match did not seem perfect. Before the pre-induction tests were performed subjects were encouraged to practise with the apparatus.

The pre-test measurements were recorded by matching upper and lower windows alternately with the left eye, right eye and binocularly using the shutter. This sequence was varied but was always repeated four times. The time taken to perform these tests varied between 0.5-1.5mins. The pre-test bias was then calculated by averaging the difference between the upper and lower settings for each condition. Subjects whose bias was high (above 0.5cm) were asked to return a few days later to check whether the bias had faded. Some astigmatic subjects, however, had a constant bias. Any orientationally linked bias of the subjects that remained was either added to, or subtracted from the post-induction readings, according to the relative polarity of the bias.

3.4.2. Induction Procedure

After the pre-test period the subject swung his chair to view the tachistoscope. He was asked to support his head on a chin rest and to position it so that each eye directly viewed a front-silvered mirror. The exposure commenced 10-30secs. after the pre-test. The fixation circles were illuminated to ensure binocular fusion of the field. The tachistoscope was then switched to automatic triggering mode. The 'on' and 'off' periods required were adjusted before the experiment began. Each field could be illuminated for different periods and have variable onset asynchron y For most experiments two identical fields were triggered simultaneously, alternating with two opposite fields which were also triggered simultaneously. The colour and orientation pairings could be easily altered by changing the colour filters or the gratings of the fields. A number of experiments used monocular stimulation only. During these experiments either the right or left fields were switched off and the unstimulated eye was covered with an eye patch. The exposure period varied with different experiments and was measured with a stop watch. The time was independently recorded on the chart recorder. During the exposure the subject was instructed to allow his gaze to move constantly around the fixation circle. This procedure allowed some standardisation of eye movements amongst subjects and ensured equal exposure to light and dark bars of the test pattern. Subjects were asked to report any afterimages during adaptation, particularly during the 'off' periods. At the end of the exposure period the subject was told to turn away from the tachistoscope and to gaze around the room, but not at the test pattern.

3.4.3. Post-induction Tests

The post-induction tests started one minute after the end of the exposure period. The one minute period was introduced for several reasons; firstly to allow subjects to become accustomed to the room lighting: secondly to remove some variability from the results; and thirdly to allow any afterimages to decay. A large aftereffect decays rapidly over the first few minutes and tests made before one minute are extremely variable. The colour match procedure was the same as the pre-test procedure. The order in which the left eye, right eye and binocular recordings were made was varied. In some experiments, however, the order of testing depended on the conditions used. Three sets of colour matches were made. The subjects were also asked for a verbal report of the test pattern. If no colour was reported subjects were requested to decide which half of the test pattern seemed to be most red or green.

Some experiments required measurement of the aftereffect over a period of time so that the decay could be studied. Recordings were taken at set intervals (see section 3.7.2.) which were measured by a stop watch. The time was also recorded by the chart recorder. To standardize the illumination the subject usually remained in the experimental room during the decay period.

3.5. Subjects

All the subjects were adult staff or students at the University of Keele. The subjects were all tested for colour vision abnormalities using Ishihara plates and for acuity using a Snellen chart. Some subjects with poor acuity were used for the experiments reported in Chapter 7. Most subjects were naive initially but learnt of the nature of the McCollough effect at some stage. All were naive as to the particular purpose of any series of experiments (except NJL).

3.6. Subject Reliability

3.6.1. Colour match settings

The reliability of a group of match settings depended upon the strength of the aftereffects measured. Strong aftereffects were generally more variable than weak aftereffects. The standard deviation for strong aftereffect was usually in the range of 10-20%. For weak aftereffects (below 2.0cm) the standard deviation was usually in the range of 10-15%. A large proportion of the deviation in the strong effects apeared to be a systematic change due to rapid decay. Pre-test readings and just detectable aftereffects had a standard deviation of 10-25%.

3.6.2. Repeatability

When experiments were repeated with the same subject the aftereffects varied in strength. Some causes of this variability were found during the course of the experiments and were then controlled. The variability changed therefore from about 12% at first to about 8% towards the end.

3.7. Decay curves

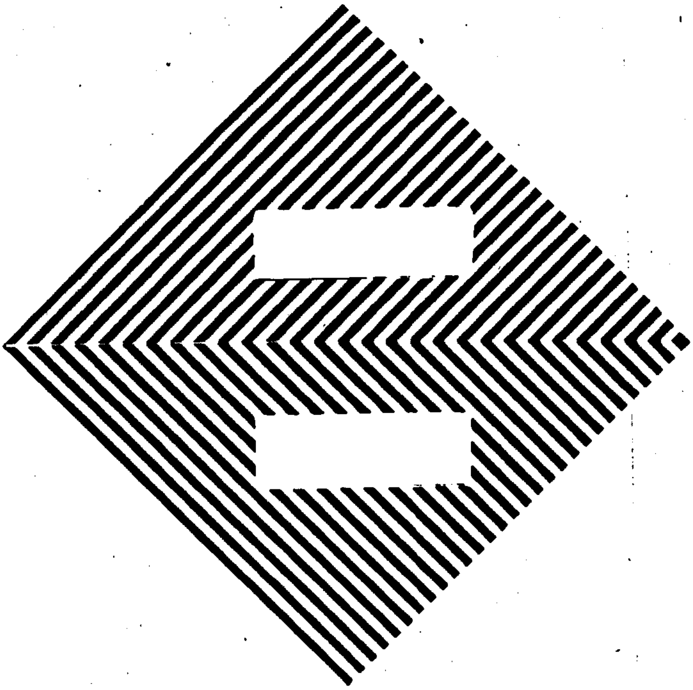
Various aspects of the decay were investigated in order to determine the validity of the 'match and null' method of measurement. The red and green components of the decay curve were also investigated. All the decays were recorded binocularly and monocularly, after an induction of 15 minutes comprising of 1 second 'on' and 4 seconds 'off' periods.

3.7.1. Comparisons of methods of measurement

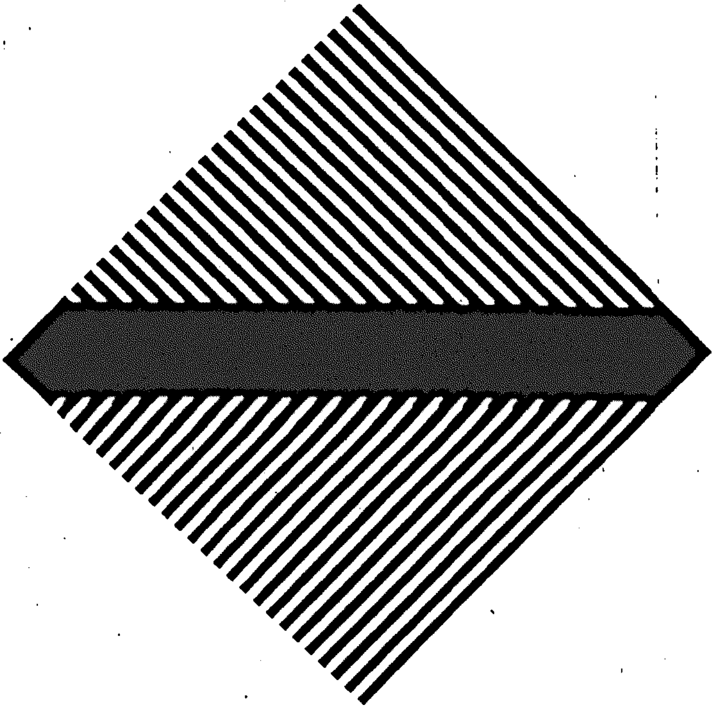
Numerous methods have been used to measure the McCollough effect. It has been claimed that the 'match and null' method leads to a 'different type of (decay) curve' which results 'from some special feature of the method' (Shute 1979). Comparisons of the 'match and null', a null and a match method, were made to investigate this claim.

The apparatus could be modified to provide a pure match or a pure null measure of the aftereffect. A match measure was provided by substituting the normal test pattern with one which had homogeneous achromatic windows (fig. 3.4a.). The windows were

Fig. 3.4.



(a) Match method test pattern



(b) Null method test pattern

matched to the surround gratings without being nulled. The decays were compared using the match and null method in one eye and the match method in the other. Since control experiments had shown that the initial strength and decay curve did not vary significantly between the two eyes for the subject used in this experiment, comparing the two eyes was a valid way of comparing the two measuring methods. The methods of measurement were reversed in a later experiment, to check for any bias produced by either eye. The results (fig. 3.5.) show that the match method gives a measurement which, as would be expected since no null measure was involved, is approximately half that given by the match and null method. The decay curves do not vary significantly.

A null measure was provided by substituting the normal test pattern with a transluscent pattern without windows. The two halves were separated by a homogeneous black bar (fig. 3.4b.). The upper and lower halves of the pattern were nulled without matching. Comparisons with the match and null method were made by using the null method in one eye and the match and null in the other. The measurement method used in each eye was reversed in a later experiment. The results (fig. 3.6.) show that the null method gives a measurement which, as would be expected since no match measure was involved, is approximately half that provided by the match and null method. The decay curves do not vary significantly.

The decay curves obtained by a match method and a null method show similar characteristics to those obtained with the match and null technique. The decay curves reported in this thesis are not, therefore, due to some peculiarity of the method used to obtain them.

Fig. 3.5. Comparison of Match and Match and Null decay measures

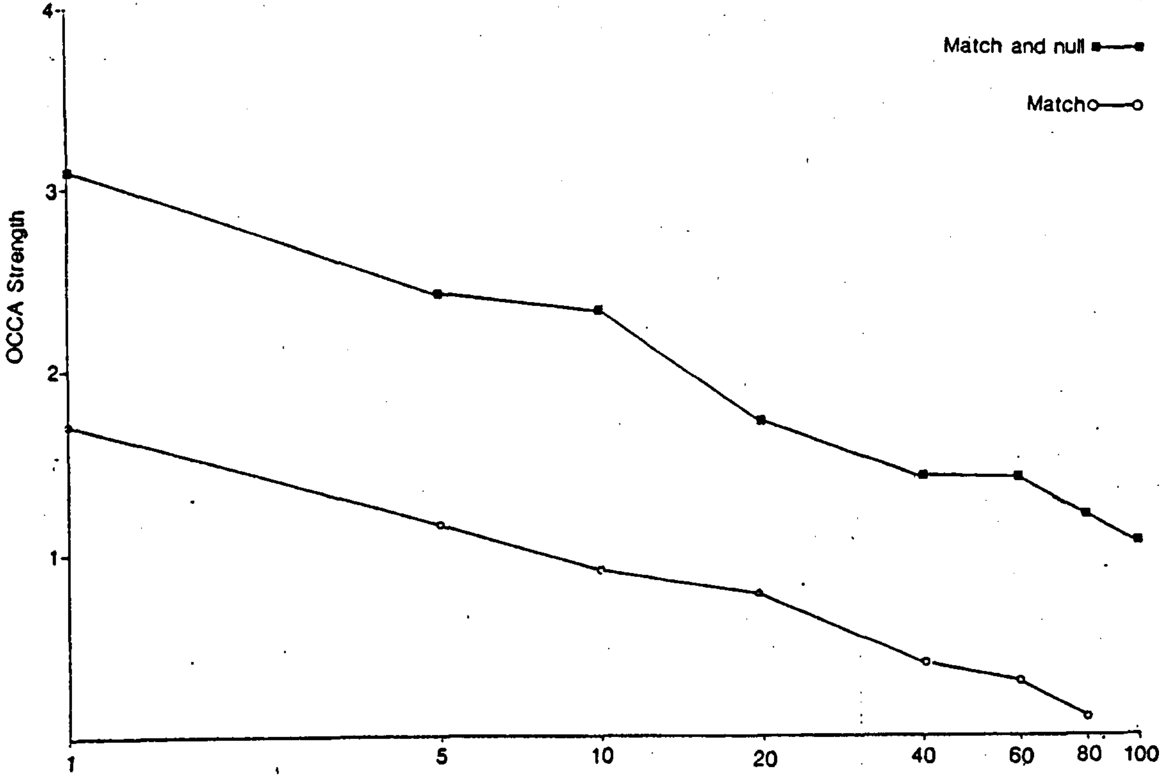
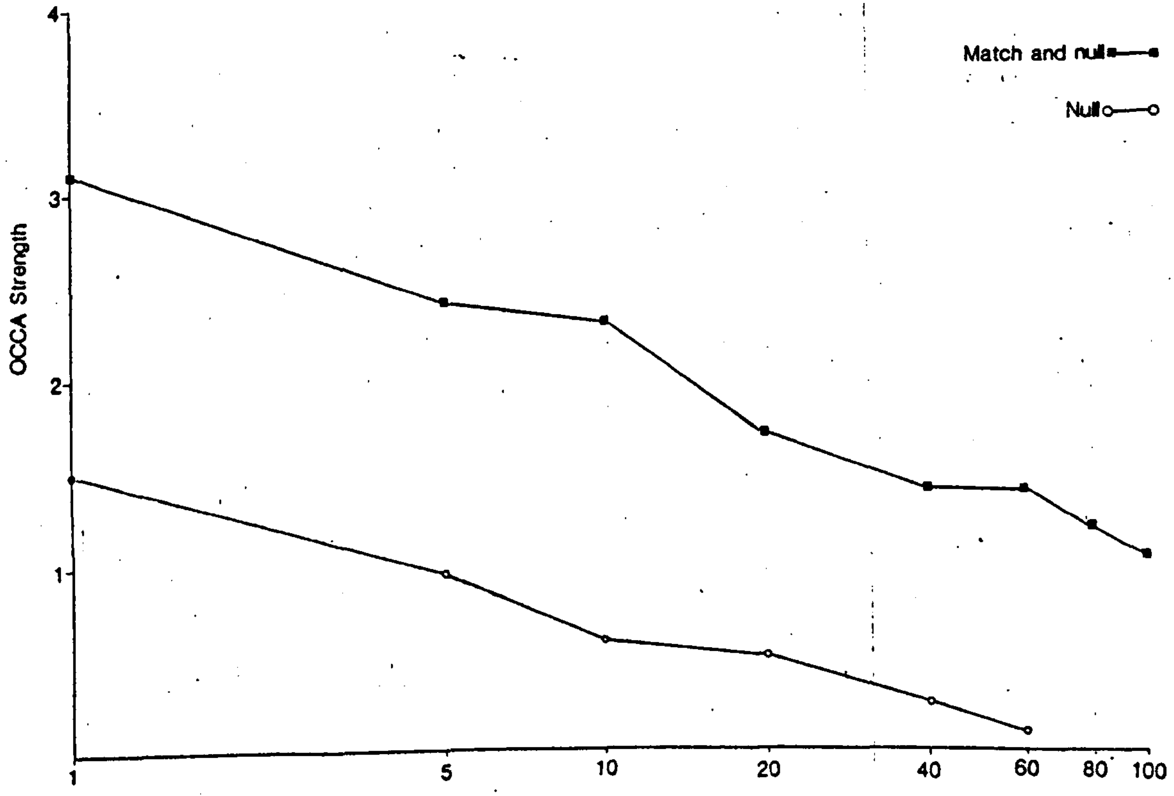


Fig. 3.6. Comparison of Null and Match and Null decay measures



3.7.2. Measurement Intervals

The decay curves reported in this thesis have been recorded by repeated testing after induction. A number of reports have indicated that testing the McCollough effect either causes or hastens its decay. Jones and Holding (1975) have compared the decay of the McCollough effect after repeated testing and time-elapse testing. They found that the repeat test procedure resulted in a linear decline of the aftereffect but the time-elapse, or delayed, test procedure resulted in little decrease of aftereffects measured up to 120hrs. after induction. When the delayed test subjects were retested they showed a greatly reduced aftereffect. Jones and Holding concluded that this was due to the first test. Skowbo, Gentry, Timney and Morant (1974) have found that exposure to achromatic gratings causes marked fading of the McCollough effect. Since the test procedure requires exposure to acromatic gratings, their results would suggest that repeated tests reduce the aftereffect strength.

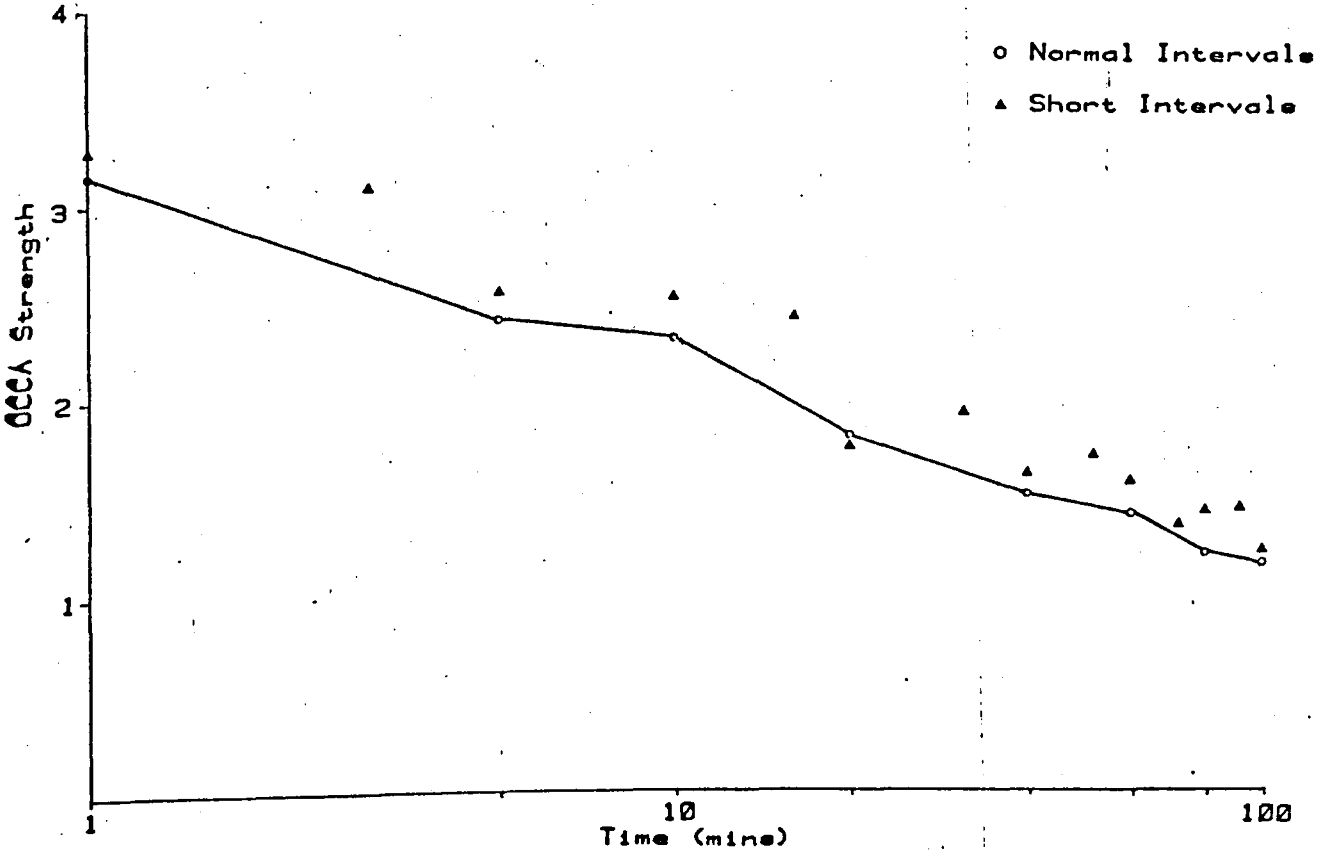
It has been suggested that the decay curve which is usually obtained in this laboratory results from the test time intervals used to measure it (Shute 1979). MacKay and MacKay (1973b) have found that a typical aftereffect decays rapidly at first and then decays at an ever decreasing rate and sometimes takes several days to fade completely. This produces curves which are straight on either log-log (MacKay and MacKay 1973b) or linear-log plots (Bradshaw 1978; White 1976). The test time intervals used in this laboratory have therefore been at 1,5,10,20,40,60,80,100 minutes and then every 100 minutes after the induction period. The claim that this results in abnormal decay was investigated by using a number of different test time intervals. Three schedules were used: one using shorter intervals of 1,3,5,10,15,20,30,40,50,60,70,80,90,100 minutes; and two using longer intervals of 1,20,60,100 minutes and 30,60,100 minutes.

The decay curves obtained for both the short (fig. 3.7.) and the long (fig. 3.8.) intervals do not vary significantly from the normal test intervals. These results show that the intervals which have been used do not unduly influence the decay. Although they do not prove that systematic differences which are due to the test procedure are not present, they do indicate that the reduction, or induction, effects are negligible. The repeated testing procedure seems to be a valid method of measurement which provides a rapid way of obtaining data. Similar results and conclusions have been obtained by White (1978) who compared his repeat test procedure with a number of delayed test results obtained after 1,4,16 and 96hrs. Although the delayed test aftereffects strengths were usually different they were 'too high' or 'too low' equally often for each decay time. White concluded that 'repeated testing seems valid for a first approximation to measuring the time course for form-contingent colour aftereffect decay'.

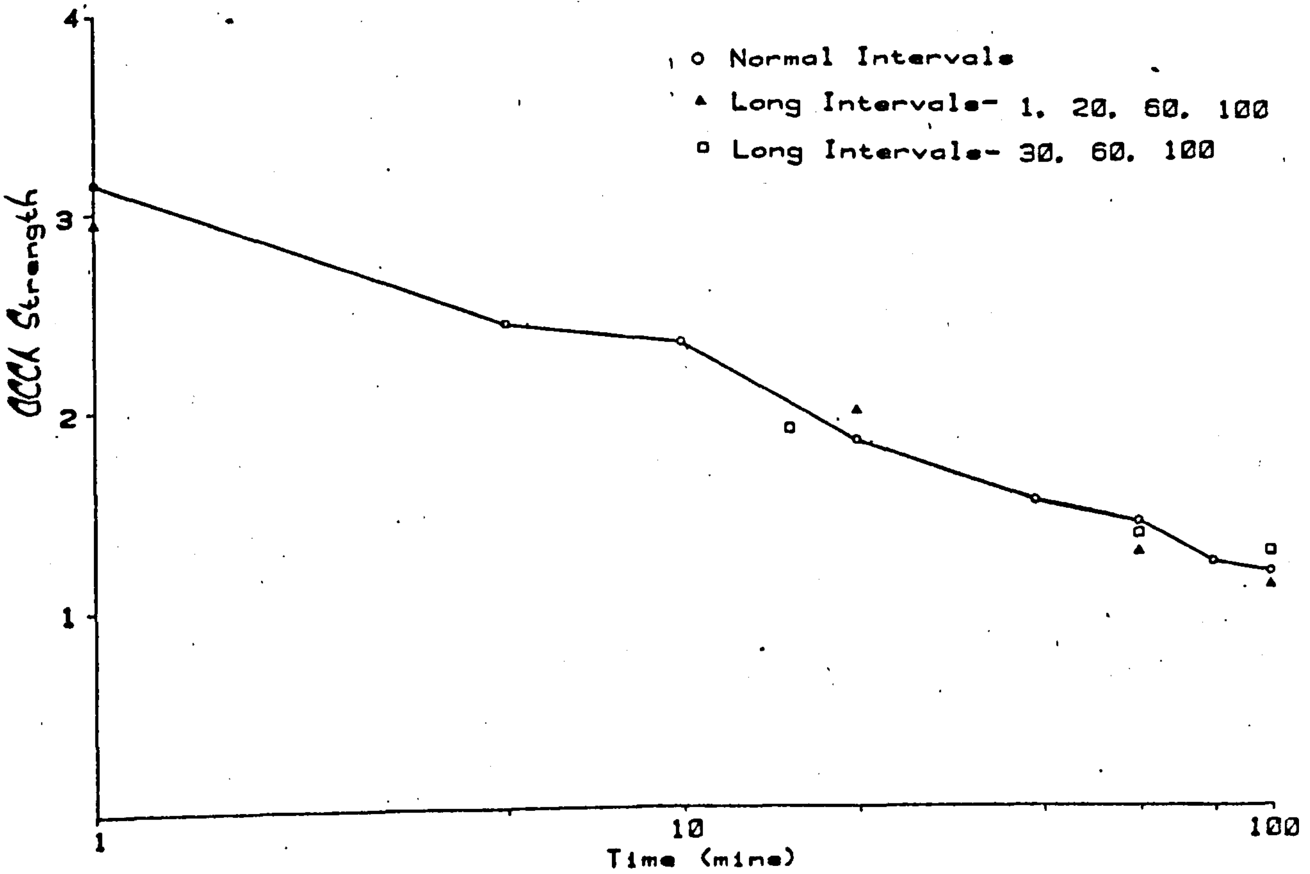
3.7.3. Red and green decay

Preliminary experiments revealed that different aftereffect strengths were produced by the red and green induction gratings. This 'slewing' effect varied between subjects in strength and polarity but usually the pink aftereffect, produced by the green gratings, was stronger than the green aftereffect. Stromeyer (1972a) has suggested that the McCollough effect consists of two components

g. 3.7. Comparison of decays produced by normal and short measurement interval



3.8. Comparison of decays produced by normal and long measurement intervals.



which decay at different rates and produce an aftereffect which decays rapidly at first then more slowly. A number of experiments were performed to investigate this suggestion.

(a) Normal Induction

It was possible to indentify the red and green components of the aftereffect using the pre-induction readings. These readings were made with little or no colour bias and represented the 'neutral' position on the chart recorder. Points to one side of the pre-induction readings represented the pink aftereffect and points on the other side represented the green aftereffect. A slight error was involved as normally the pre-test registered an initial bias of 0.1-0.3cms and the three or four readings were scattered in a range of 0.2-0.5cms. The neutral position was taken as the mid point of the scatter and therefore could have been mis-placed by a few millimeters. However, this was only 0.1-0.5% of the initial strength. The results (fig. 3.9.) for two subjects show that the pink aftereffect is slightly stronger than the green, but the decay curves do not vary significantly. Most subjects reported verbally that the pink hue of the aftereffect was more vivid than the green. Stromeyer (1969) has noted that after induction with various filters, the red aftereffect is the most commonly reported.

(b) One Colour Induction

Stromeyer (1969) has shown that McCollough effects can be produced by using one colour with one orientation pattern. In order to study the slewing effect more closely, one colour and orientation was presented to one eye and the opposite pairing was presented to

Fig. 3.9.

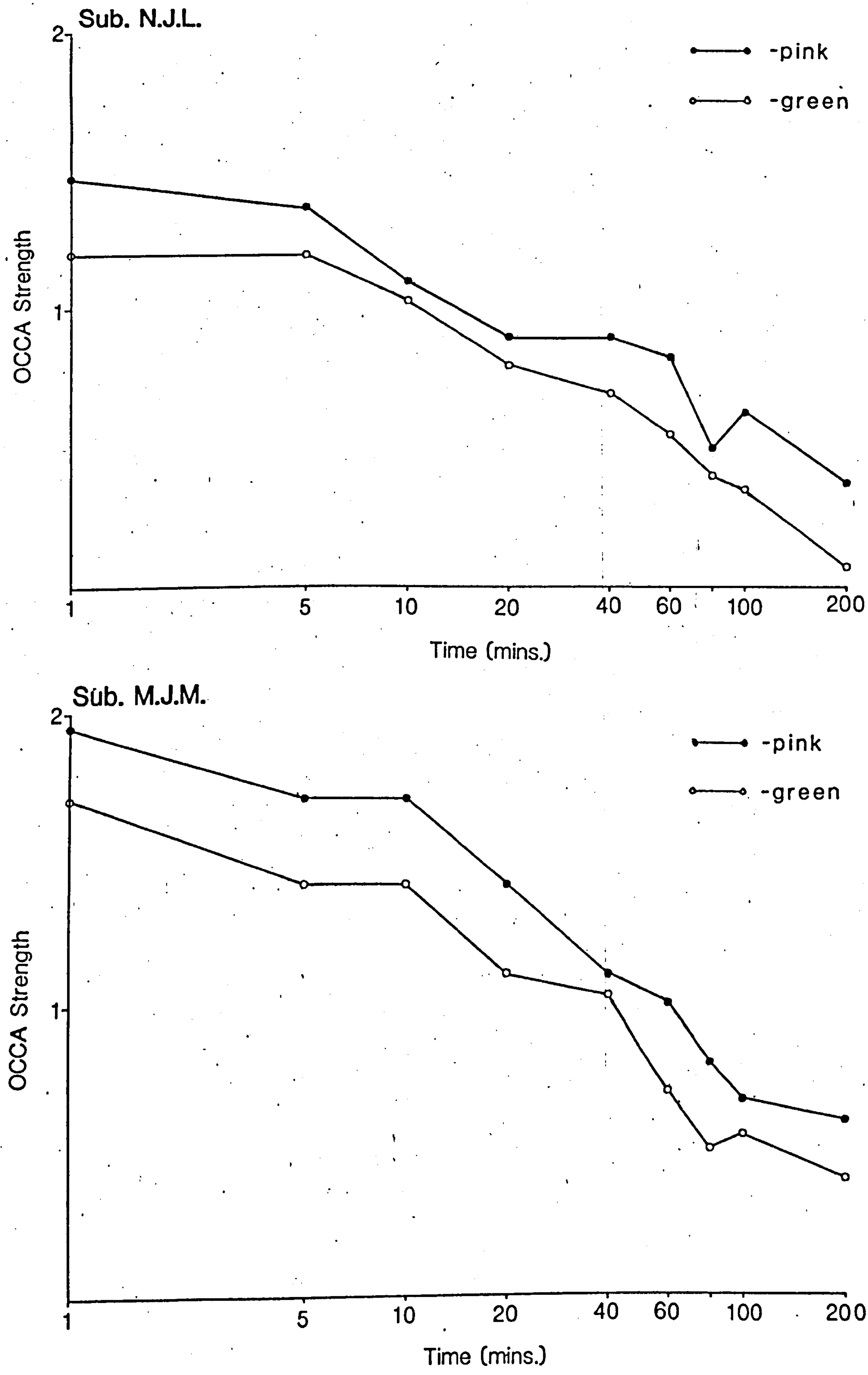
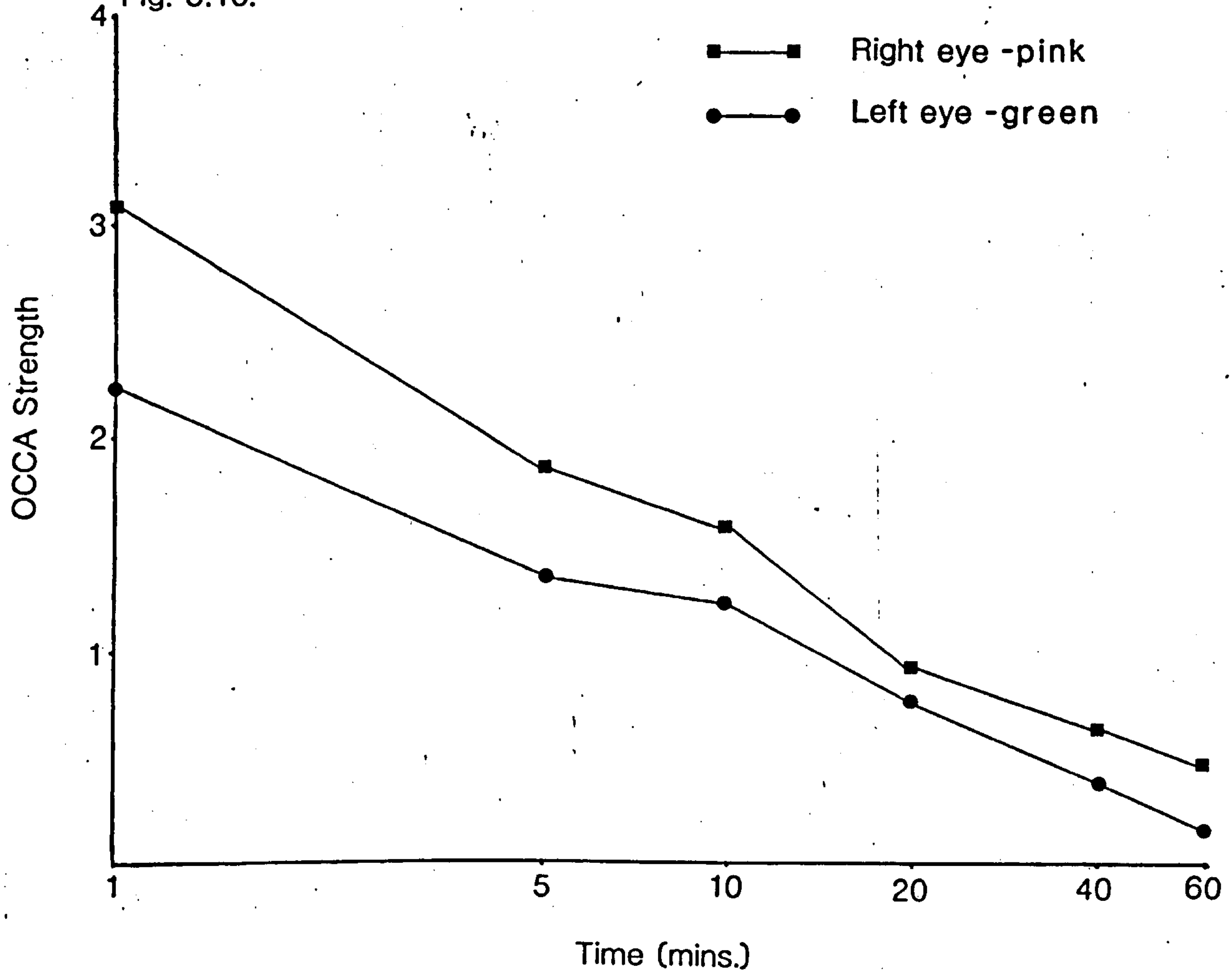
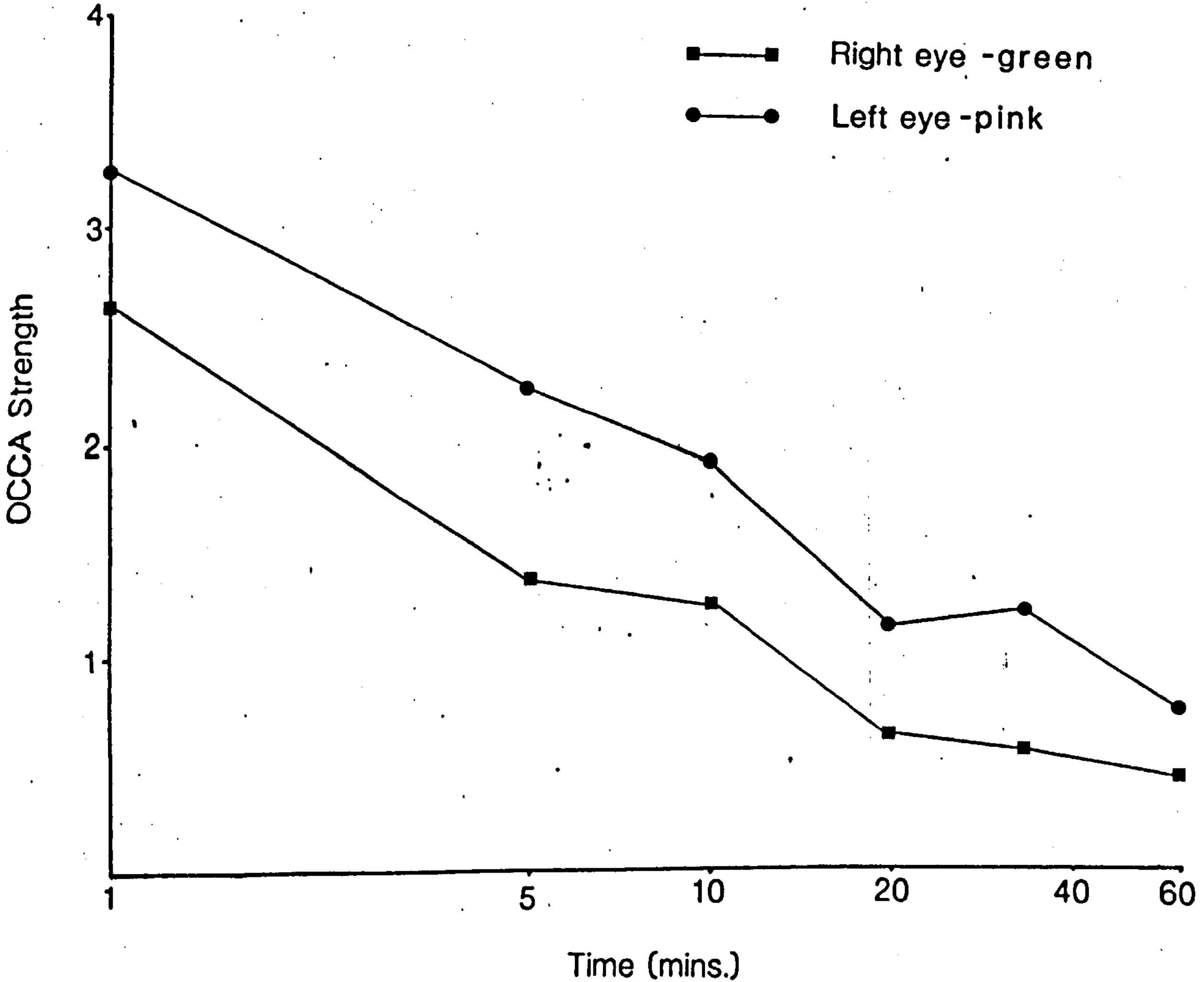

Sub. N.J.L.
2
1
OCCA Strength
-pink
-green
1
5
10
20
40
60
100
200
Time (mins.)
Sub. M.J.M.
2
1
OCCA Strength
-pink
-green
1
5
10
20
40
60
100
200
Time (mins.)

Fig. 3.10.


■—■ Right eye -pink
●—● Left eye -green
OCCA Strength
4
3
2
1
1
5
10
20
40
60
Time (mins.)


■—■ Right eye -green
●—● Left eye -pink
OCCA Strength
4
3
2
1
1
5
10
20
40
60
Time (mins.)

the other. The stimuli were presented in the reverse arrangement in a later experiment to enable any bias produced by either eye to be removed. The results (fig. 3.10.) show that no bias was produced by the eyes and although the pink aftereffect is higher, the decay curves are not significantly different. The difference in the initial strength of the red and green components, therefore, does not alter the overall shape of the decay curves.

3.8. Terminology.

The strength of the aftereffect throughout the rest of the thesis will be described simply as a number. This number represents the average number of centimeters between the recorder pen marks for each condition (i.e. an average strength of 2.6cms will be referred to as 2.6). Decay measurement times refer to the time from the end of the induction period not from the beginning.

CHAPTER 4 EXPLORATORY EXPERIMENTS

4.1. Introduction

The main body of the research reported in this thesis stemmed from observations regarding the variability of results in some preliminary experiments on the McCollough effect. Because of the scale of this variability, it was decided to look for factors which appeared to have a systematic effect on the decay or the strength of the OCCA. Although the early experiments were not designed to investigate variability, many extraneous factors which might have affected the aftereffect were recorded.

The experiments, initially suggested by Prof. D.M. MacKay, followed on from thesis work by Dr. K. Bradshaw (1978). These had three concerns: the effect of altering the temporal characteristics of the induction period; differences between monocular and binocular aftereffects; and the build-up of the aftereffect. They will be briefly described in order to illustrate the variability which emerged.

4.2. Controlled factors

In all the experiments reported in this chapter, certain factors were controlled, or recorded, because previous research had shown that they could affect the characteristics of the McCollough effect.

All experiments were conducted in a room of constant low luminance (4mlm) and subjects were exposed to this illumination

10mins. before the experiment began, as well as during the pre-test, induction and post-induction phases. Induction and test gratings were at constant luminance, as it has been noted that high luminance induction gratings with low luminance test gratings produce higher aftereffects (White, 1976). It has also been demonstrated that high luminance gratings, presented before or after induction, reduce the OCCA strength (Skowbo et.al., 1974; Skowbo and Clynes, 1977; Skowbo, 1979). MacKay and MacKay (1976) have shown that total darkness arrests the decay of the McCollough effect. In all aspects of the experiments constant luminances were found to be essential to reduce variability.

The 'on' and 'off' intervals of the induction period were also carefully monitored since Bradshaw (1978) has shown that changes in either of these intervals affects both the strength and the decay of the aftereffect. The duration of the induction period was fixed for each set of experiments. Decay measurements were made at fixed intervals (see Section 3.7.2.) but although they began at the same time there was some variation in the time taken to do them.

Another factor thought likely to cause variation in the McCollough effect was diet. It has been shown, for example, that various drugs, including such common agents as caffeine and nicotine, affect both the decay and the strength of the aftereffect (Shute, 1978; Amure, 1978, 1979). The subject's diet was not controlled, but various aspects of it, including any medication, were recorded. Most experiments were performed in the morning to reduce the possibility of diet variation.

4.3. Temporal characteristics of the Induction Period

The experiments recorded in this section were performed in order to analyse the effect of varying the 'on' and 'off' intervals of the induction period.

(a) Intersubject

A number of subjects were used for several of these runs, all of whom had normal, or corrected, acuity and normal colour vision. Table 4.1 shows the initial OCCA values for 4 subjects after various induction sequences.

Table 4.1.

SUBJECT		NJL	MJM	RJM	NM	MEAN	S.E
INDUCTION SEQUENCE							
ON	OFF						
0.1	1.9	1.4	1.7	0.5	1.3	1.23	0.26
0.2	1.8	1.6	1.7	1.1	1.3	1.43	0.14
0.4	1.6	2.3	3.0	2.6	2.8	2.68	0.15
0.8	1.2	1.5	3.1	4.5	2.5	2.9	0.63
1	1	2.1	5.6	2.9	2.1	3.1	0.32
0.1	0.1	0.6	1.8	--	--	1.2	0.60
0.1	1	0.8	1.2	--	--	1.1	0.26

The above table shows large differences in the initial OCCA for all the induction sequences although the conditions were identical for each subject. These differences were not always consistent. For instance, though in general subject MJM had larger OCCA's than the other subjects, on one occasion (using induction sequence of 0.8s 'on' and 1.2s 'off') subject RJM developed a substantially higher aftereffect. This difference in variation between subjects occurred many times in the exploratory experiments. Fig. 4.1 shows the decay curves of the McCollough effect for the 4 subjects after 4 different induction sequences. These also show large and inconsistent variations.

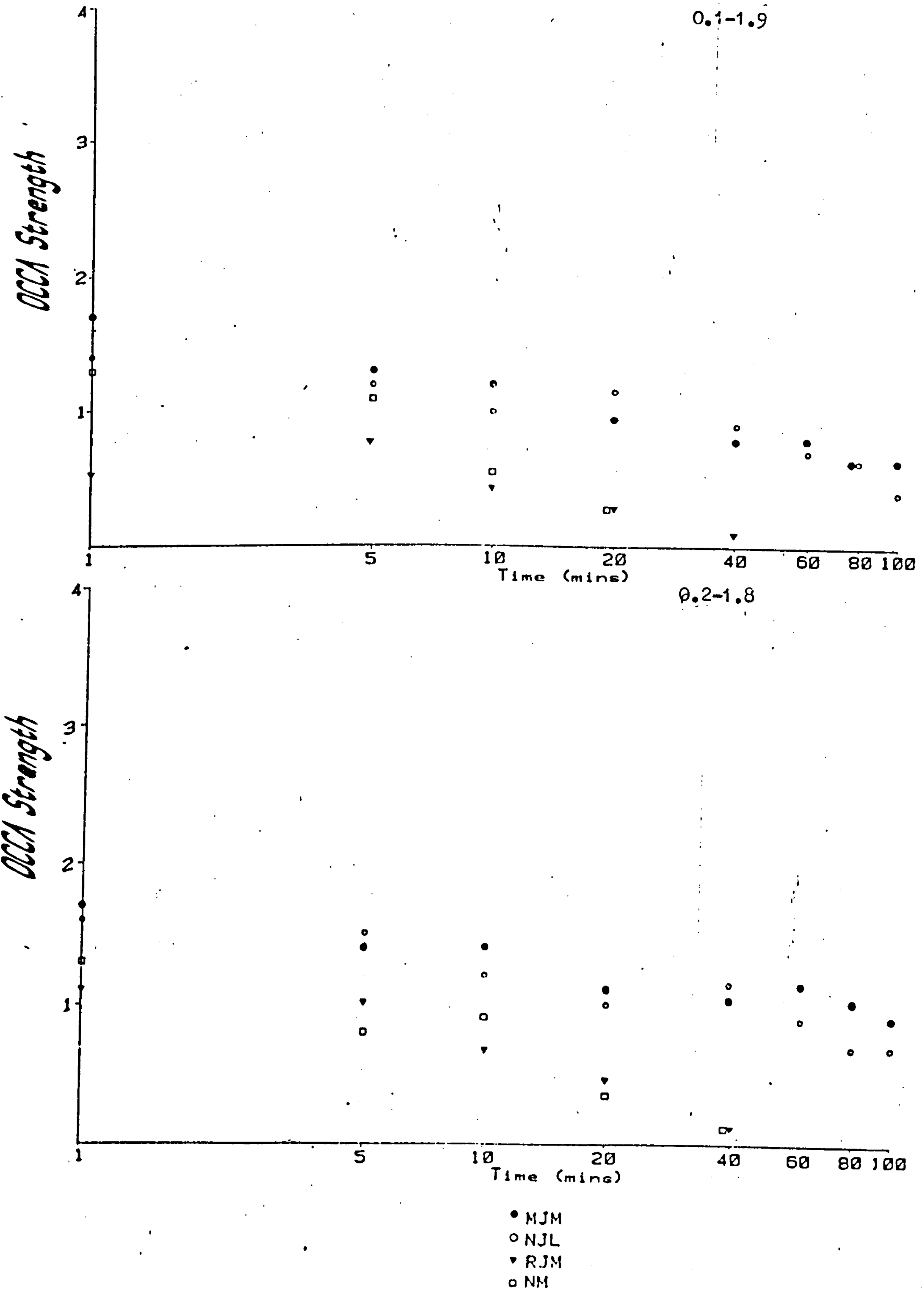
(b) Intrasubject

Two subjects repeated some of the experiments a number of times and the initial strengths of the repeated runs are shown in table 4.2

Table 4.2.

INDUCTION SEQUENCE		SUB. NJL				MEAN	S.E.
ON	OFF						
0.1	1.9	0.9	1.3	0.8	1.4	1.1	0.15
0.2	1.8	1.1	1.6	1.2	1.7	1.4	0.15
0.4	1.6	1.5	2.3	2.5	---	2.1	0.31
0.8	1.2	3.4	3.6	3.0	3.4	3.35	0.12
		SUB. MJM					
0.1	1.9	2.3	1.7	1.1		1.7	0.35
0.2	1.8	2.3	1.3	1.1		1.77	0.3
0.4	1.6	3.0	1.3	1.7		3.03	0.66
0.8	1.2	3.1	3.3	3.1		3.17	0.06

Fig. 4.1. Intersubject variability of the OCCA decay



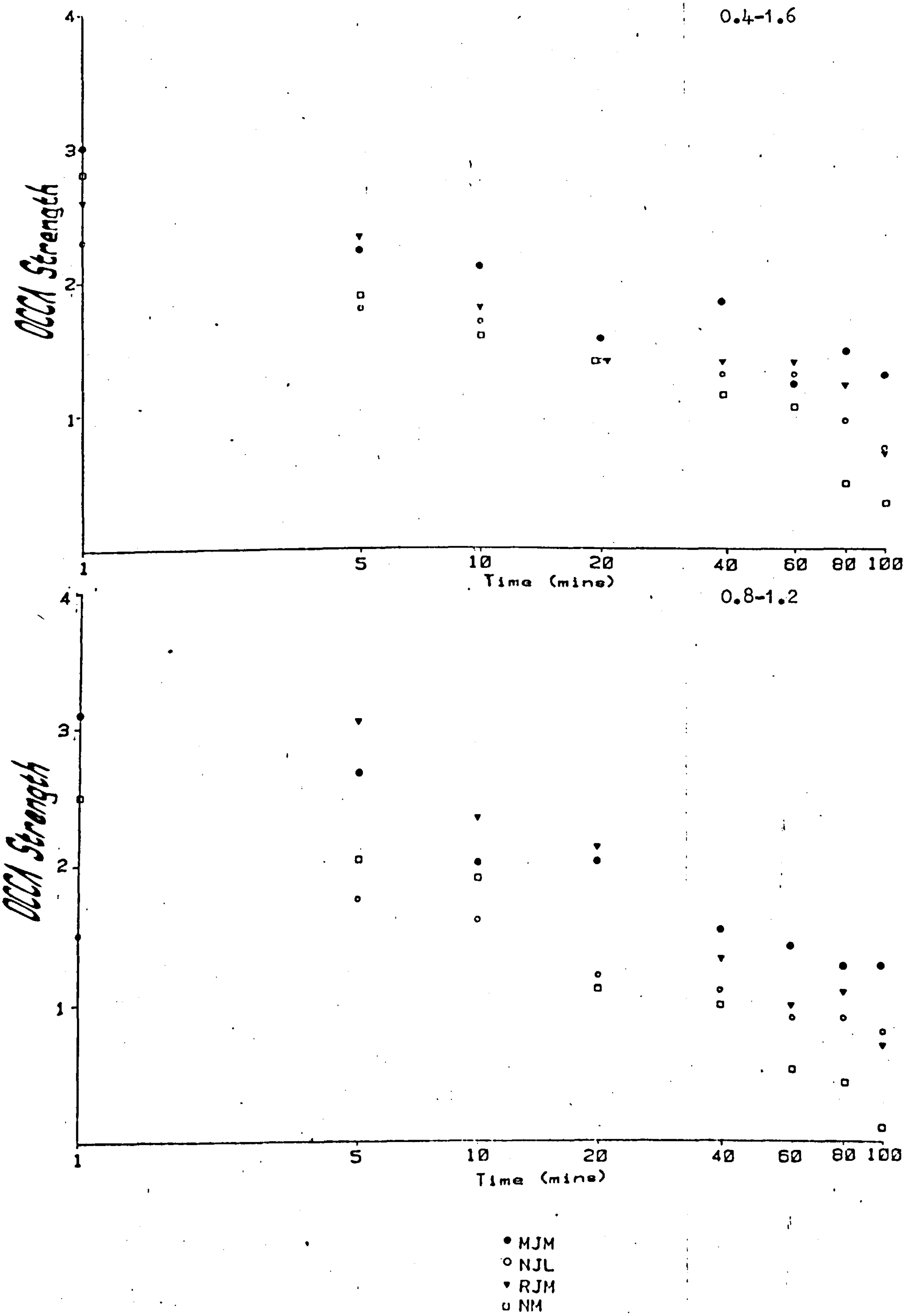

0.4-1.6
OCCA Strength
4
3
2
1
1
5
10
20
40
60
80
100
Time (mins)
0.8-1.2
OCCA Strength
4
3
2
1
1
5
10
20
40
60
80
100
Time (mins)
● MJM
○ NJL
▼ RJM
□ NM

Table 4.2. shows that each subject displays a range of variability for every induction sequence, even though the conditions for each sequence were identical. This range of variability is typical for all the early experiments. The results indicate that the longer 'on' period of 0.8s was associated with less variability for both subjects. Some selected decay rates for the 2 subjects are shown in Fig. 4.2, and these also show intrasubject variability. Since the subjects were kept in a room of constant luminance while the decay was recorded, there was no obvious explanation for these results.

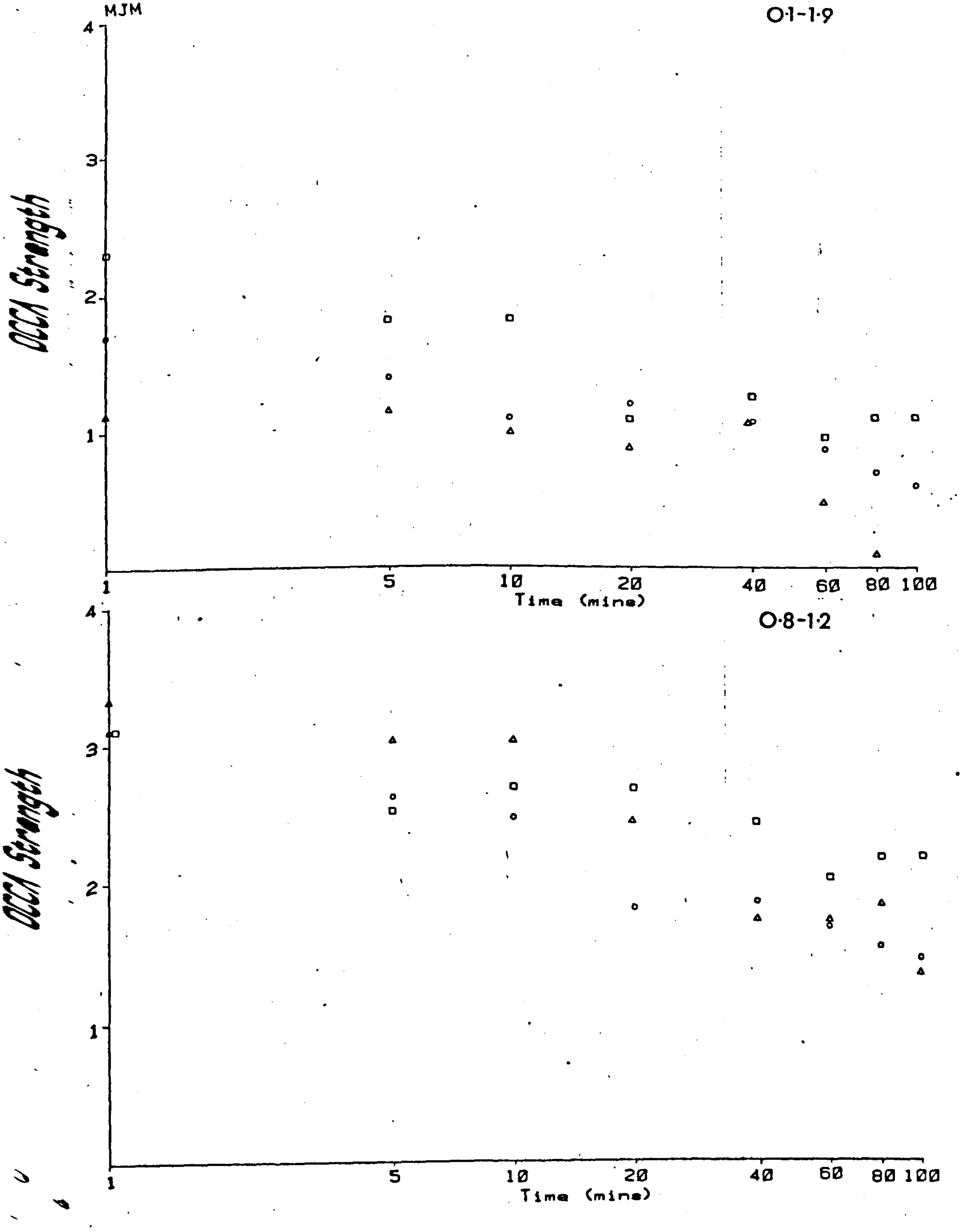
4.4. Build-up of aftereffect strength

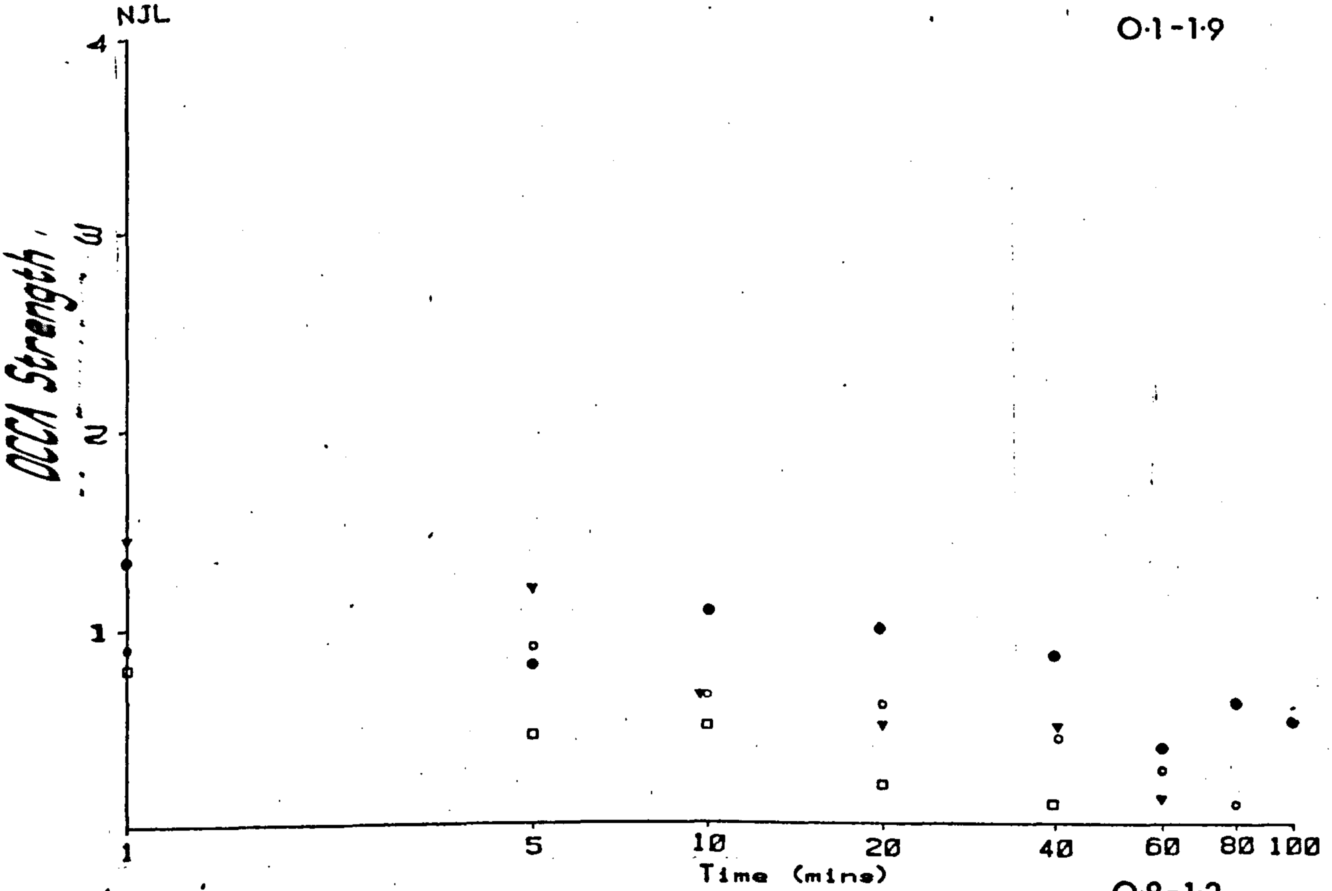
Experiments were performed to investigate the build-up of the aftereffect, using various induction periods. Like the experiments in Section 4.3., they show large differences in the initial strength and decay, but also illustrate the variability of the build-up of the McCollough effect.

(a) Intersubject

In these experiments the induction period was varied in length from between 5 and 30 mins. A constant induction sequence of 1s 'on' and 4s 'off' intervals was used. The initial strength after each induction duration for 4 subjects is shown in table 4.3.

Fig. 4.2. Intrasubject variability of the OCCA decay




NJL
O·1-1·9
OCCA Strength
1
2
3
4
1
5
10
20
40
60
80
100
Time (mins)

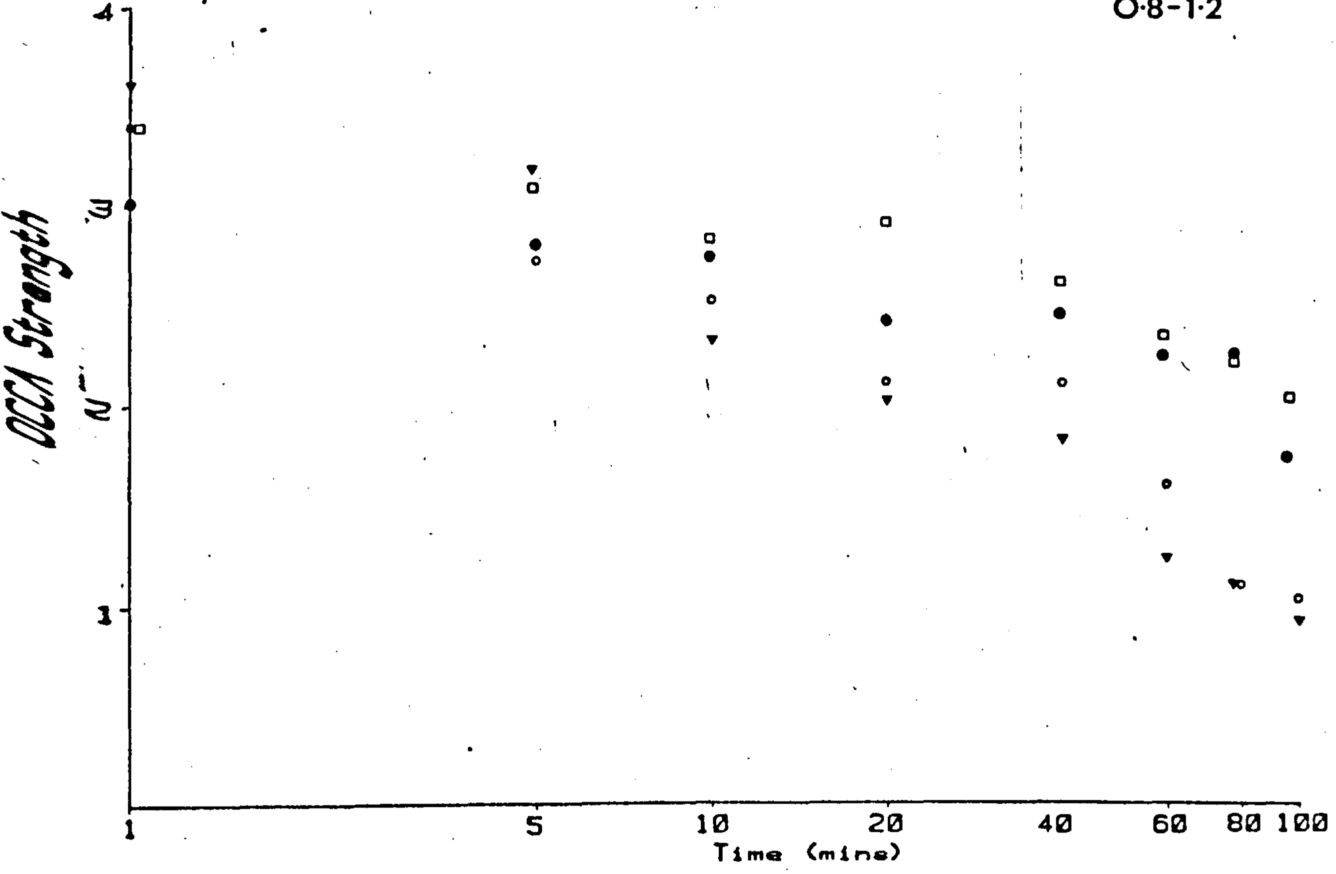

O·8-1·2
OCCA Strength
1
2
3
4
1
5
10
20
40
60
80
100
Time (mins)

Table 4.3.

SUBJECT INDUCTION DURATION	MJM	NJL	GC	RJM
5	2.1	2.1	2.4	2.95
10	2.67	2.37	3.1	3.13
20	2.8	2.43	4.13	3.87
30	3.83	3.05	4.05	3.7

The results again show intersubject variability in the initial strength as well as individual differences in the way the OCCA strength builds up. Two subjects have slightly lower initial strengths after 30 mins. than 20 mins. which suggests that they have reached a 'saturation' level. The other two subjects however, show no signs of reaching a saturation level, since the aftereffect is greater at 30 mins.

(b) Intrasubject

The sequence of experiments reported above were repeated by one subject MJM 3 times and these results are shown in table 4.4.

Table 4.4.

INDUCTION DURATION				MEAN	S.E.
5	2.07	2.1	2.55	2.24	0.16
10	2.1	2.67	3.05	2.6	0.27
20	2.9	2.8	3.9	3.2	0.35
30	3.83	4.07	3.63	3.84	0.12

These results show intrasubject variability for each induction period. Build-up of the aftereffect in another subject was studied by measuring the strength at set intervals during the induction period. The length of the induction period was varied between 2 and 32 mins. and the McCollough effect was measured at intervals of 2,4,8,16 and 32 mins. for the longest periods and at appropriate intervals for the shorter periods. The sequence of experiments was repeated randomly 3 times and the results are shown in table 4.5.

Table 4.5

INDUCTION DURATIONS				MEAN	S.E.
2	1.3	1.7	1.6	1.57	0.12
2,4	1.45	2.3	2.33	2.03	0.28
2,4,8	1.9	1.87	2.43	2.06	0.18
2,4,8,16	2.3	3.26	3.03	2.86	0.28
2,4,8,16,32	3.8	3.77	3.7	3.76	0.03

The results again show large intrasubject variability and that the aftereffect does not always build up in the same way. The variability of the build-up can be seen more clearly in graph form (Fig. 4.3.).

Both subjects show that the longest periods of induction are associated with less variability of the results.

4.5. Monocular and Binocular results

A number of investigators have indicated that monocular and binocular McCollough effects vary slightly in strength and decay slope (MacKay, 1978). The experiments reported in this section were performed to clarify some of these variations. Monocular and binocular strengths were measured after 15 mins. of binocular induction, comprising various 'on' and 'off' sequences. Since intrasubject and intersubject variability have already been illustrated in the previous sections, this section will be used to show how some runs, or sets of runs, could even show a reverse trend to previous results.

Two subjects repeated four induction sueqences a number of times. The induction sequences of 0.1s 'on', 1.9s 'off'; 0.2s 'on, 1.8s 'off'; 0.4s 'on', 1.6s 'off'; and 0.8s 'on', 1.2s 'off' were presented binocularly and tested both binocularly and monocularly. Figure 4.4. shows a summary of the inital strengths.

In general it was found that with short 'on' periods (0.1 and 0.2s) initial binocular test strengths were lower than results for monocular tests. The longest 'on' period (0.8s) produced higher binocular than monocular results. A few of the results (cross-hatched in the diagram) show a reverse in this trend. Some

Fig. 4.3. Variability of the build-up of the OCCA

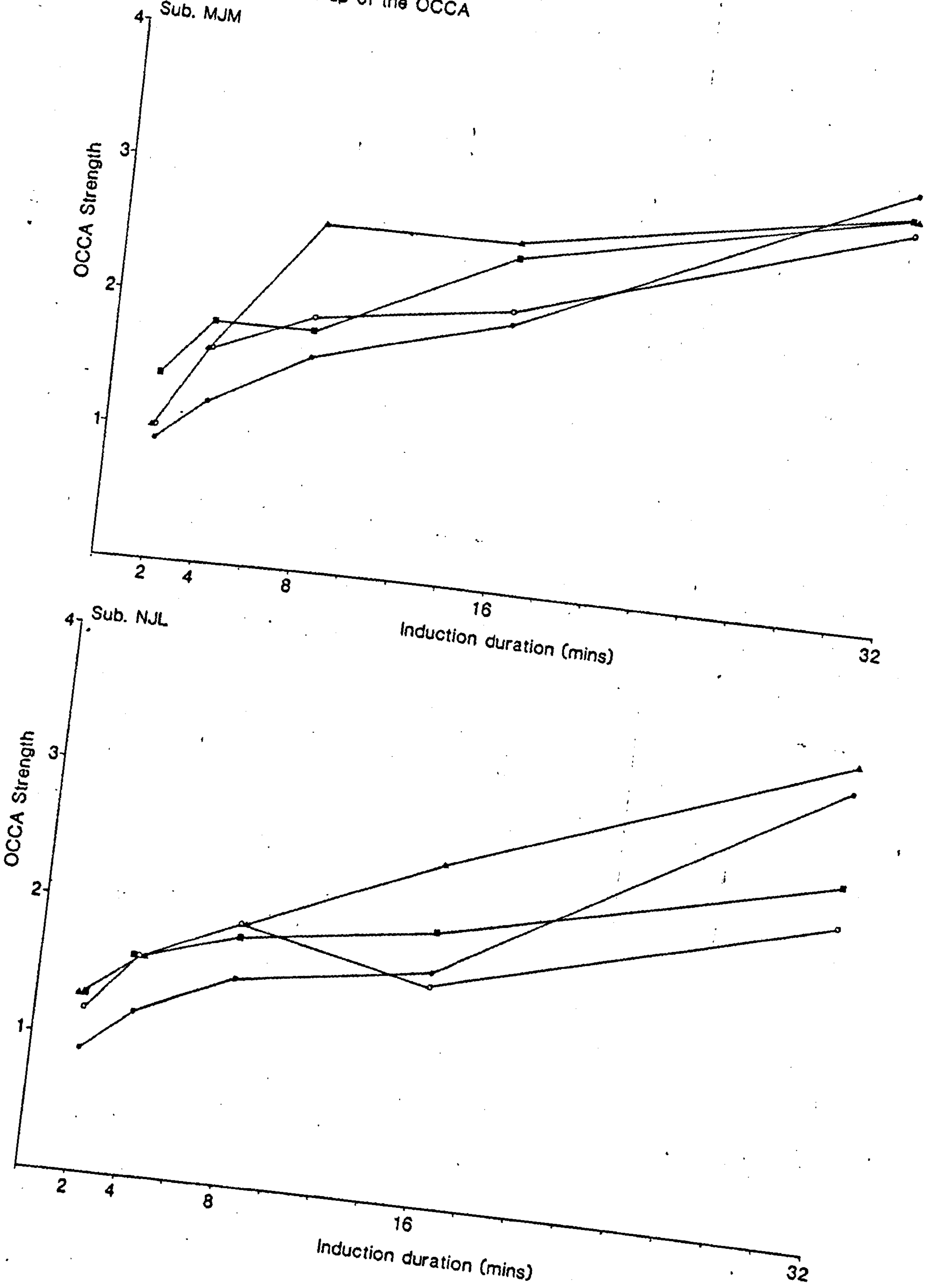
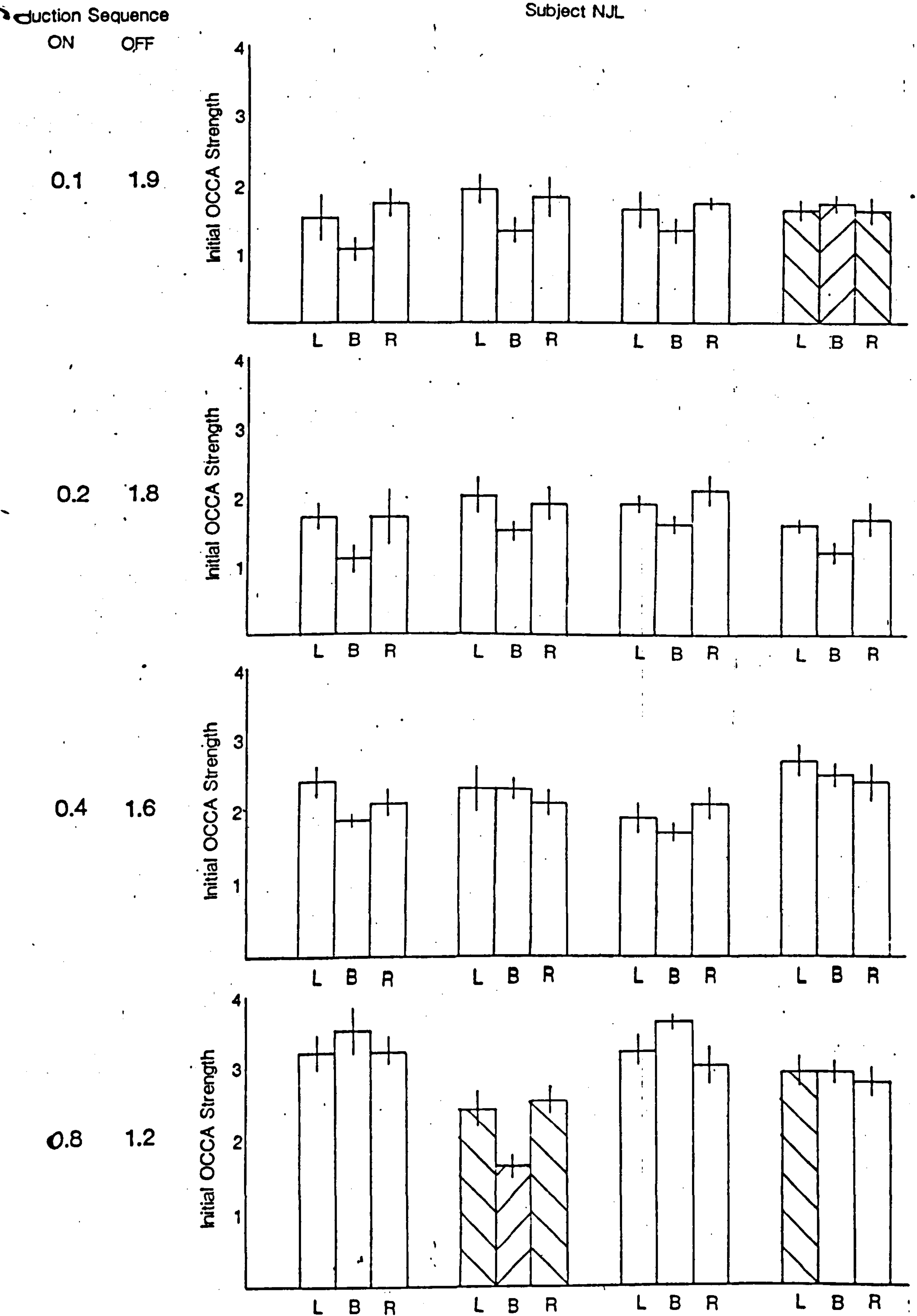
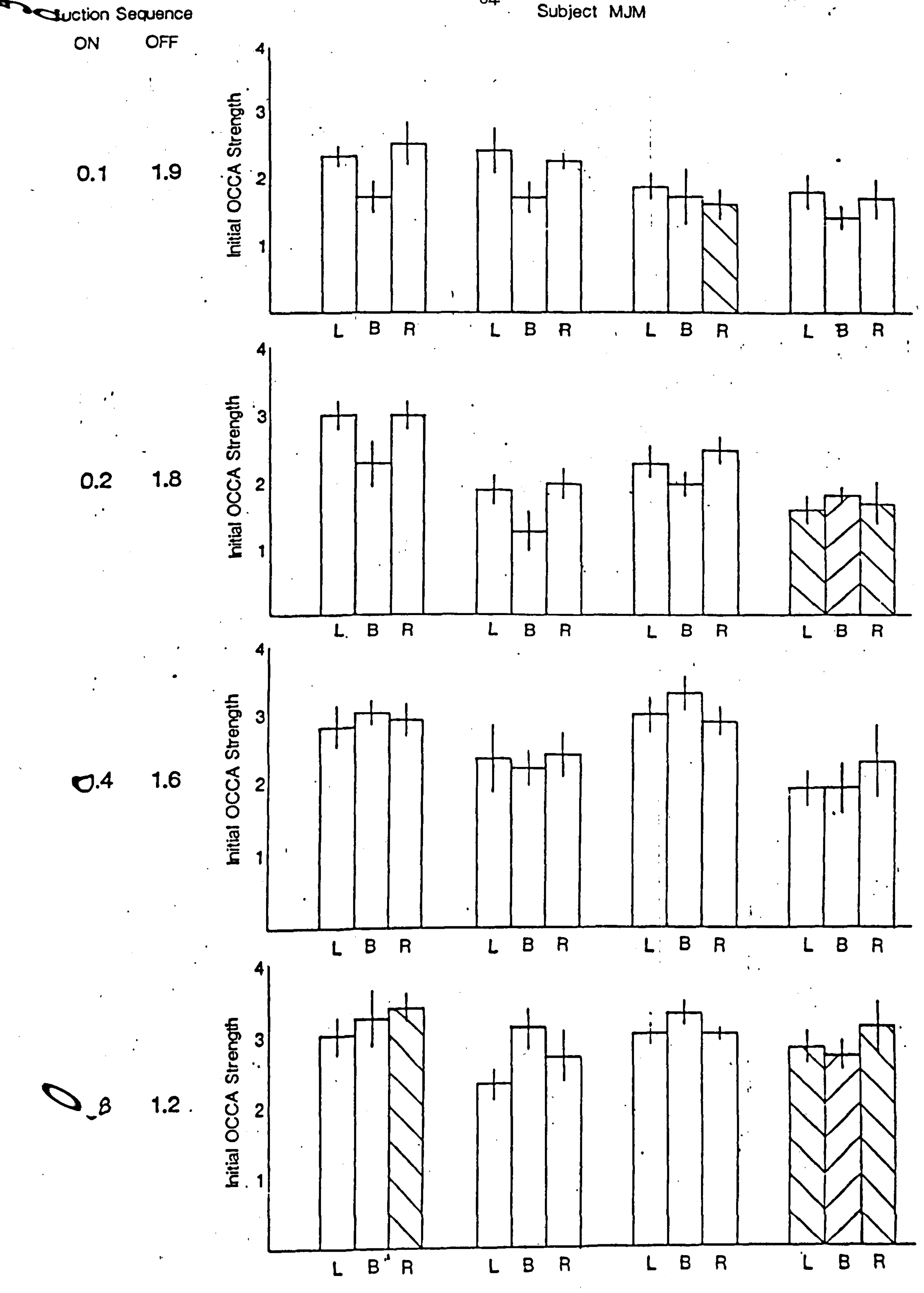


Fig. 4.4. Intrasubject variability of binocular and monocular test results





Subject MJM

uction Sequence
ON
OFF
0.1
1.9
0.2
1.8
0.4
1.6
.8
1.2
Initial OCCA Strength
1
2
3
4
L
B
R

of the results reveal quite considerable variations in the initial strength.

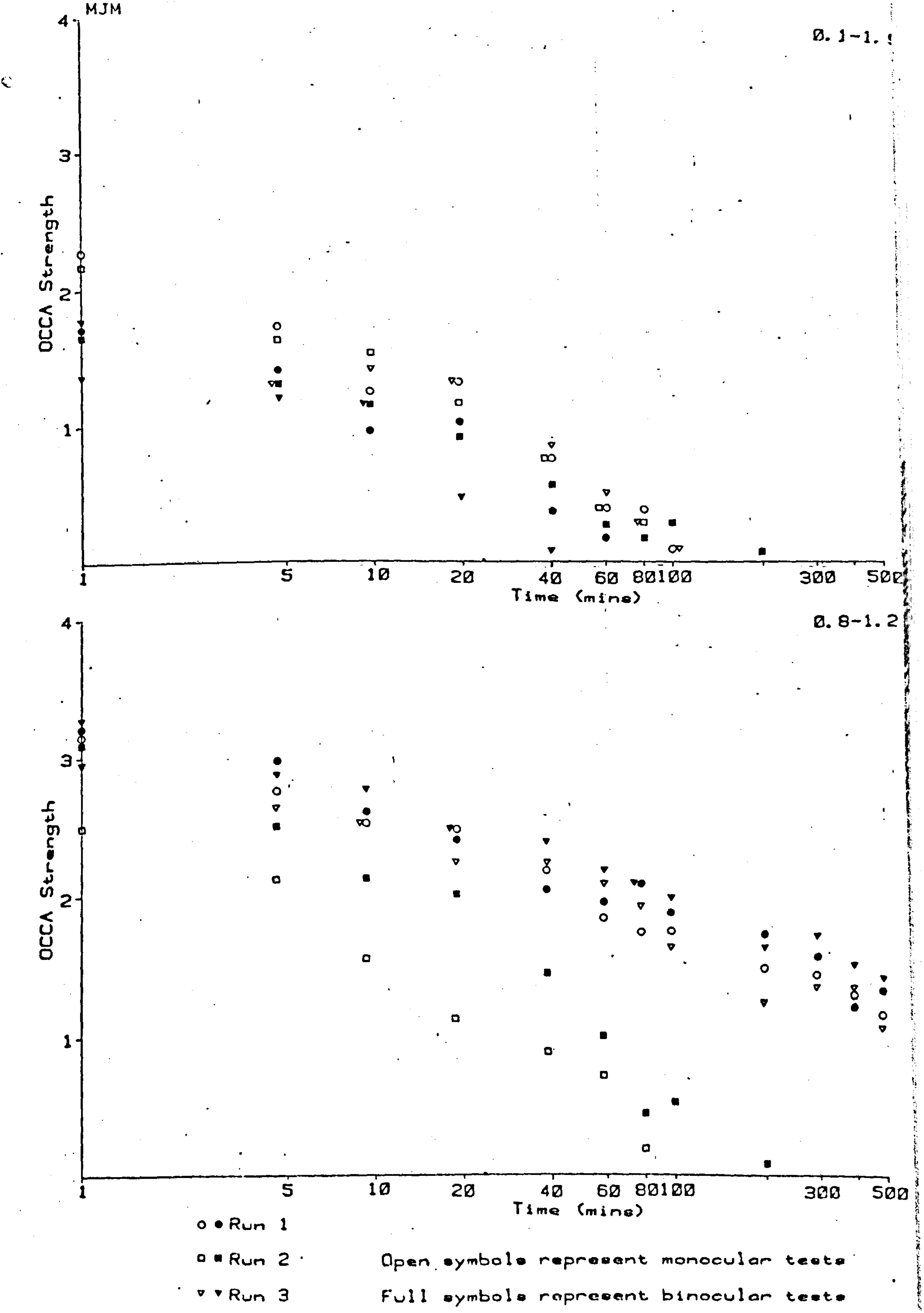
The decay rates of the monocular and binocular tests are shown in Fig. 4.5. The graphs indicate that the rates of decay were very similar for each test condition and both showed slower decay rates when the induction period consisted of longer 'on' periods. However, both subjects show one sequence of runs where this trend is reversed. If each subject's results are 'pooled' the aberrant result reduced the significance of the other results considerably.

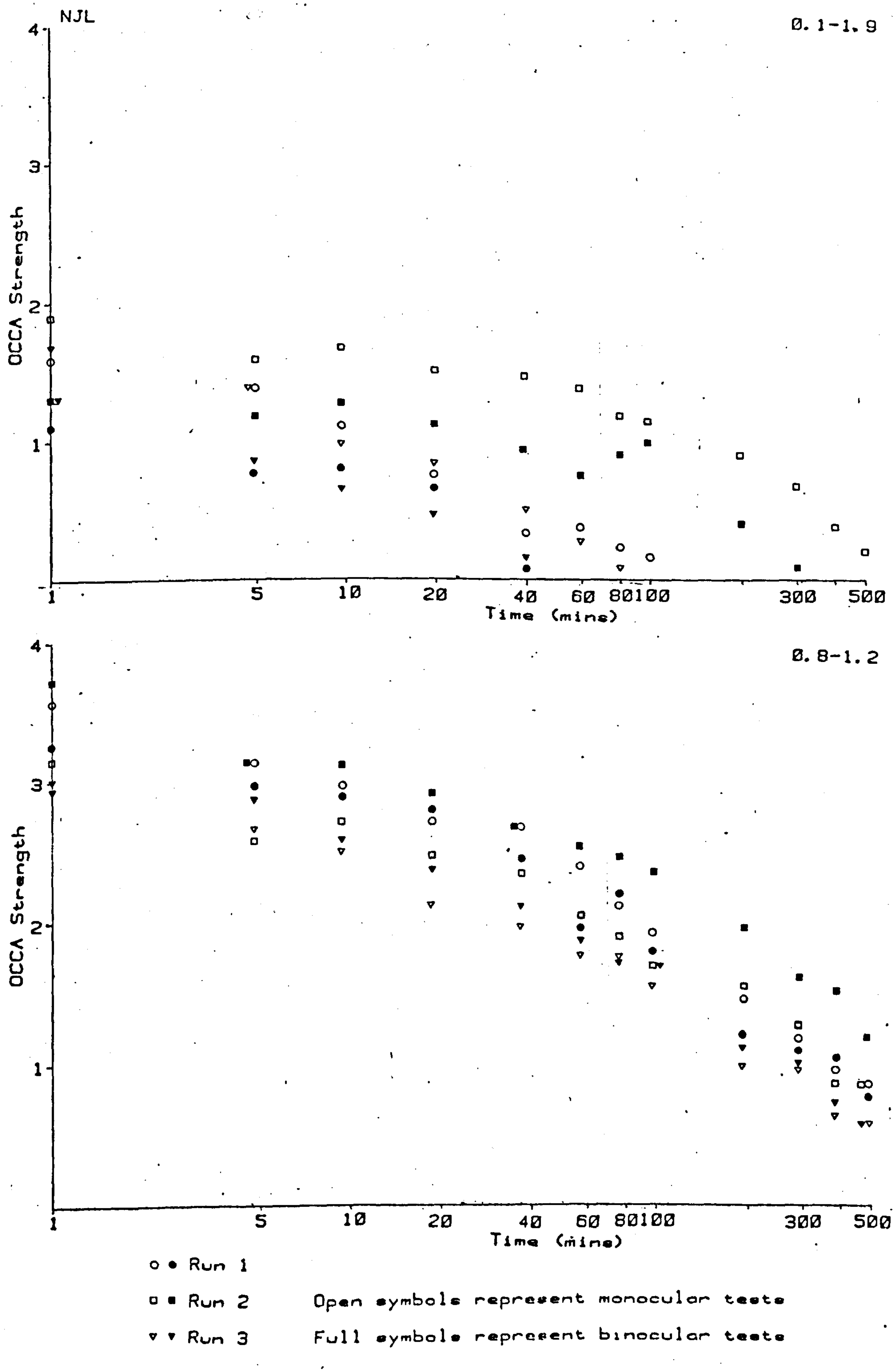
4.6. Conclusions

The preliminary experiments reported in this chapter have shown considerable intra and intersubject variability in the initial strength, the decay and the build-up of the McCollough effect. In addition, they have illustrated how a few results can obscure or negate trends which have emerged from a large number of experiments. The variability of these experiments caused a shift in emphasis in the research. Later experiments were performed to isolate some of the factors causing this variability. In identifying these factors it was hoped that the experiments would give further indications of the nature of the McCollough effect.

These preliminary experiments also demonstrated a number of useful points for further research. They showed that induction periods consisting of relatively long 'on' and 'off' periods of 1s or more produced less variable and larger aftereffects. Other experiments have shown that long 'on' and 'off' periods produce larger OCCA's (Bradshaw, 1978). For this reason most of the

Fig. 4.5. Intrasubject variability of monocular and binocular decay




NJL
0.1-1.9
OCCA Strength
4
3
2
1
1
5
10
20
40
60
80100
300
500
Time (mins)
0.8-1.2
OCCA Strength
4
3
2
1
1
5
10
20
40
60
80100
300
500
Time (mins)
○ ● Run 1
□ ■ Run 2
▽ ▼ Run 3
Open symbols represent monocular tests
Full symbols represent binocular tests

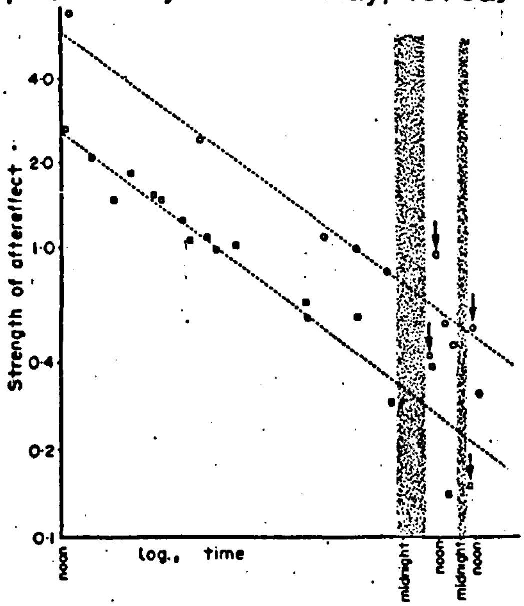
experiments reported in this thesis have used 1s 'on' and 4s 'off' intervals during induction. The build-up experiments showed that the variability of the McCollough effect was higher below 10-20 mins. of induction and that longer periods of induction produced more stable aftereffects. However, some subjects showed signs of reaching a saturation level after 20 mins. of induction. Therefore the duration of the induction period was set at 15 mins. in order to give the maximum stability without saturation. Finally, the binocular and monocular experiments indicated that when the McCollough effect was induced binocularly, most subjects developed similar monocular aftereffect strengths which decayed at nearly indentical rates in each eye. This observation was used for the experiments reported in Chapters 8 and 9.

CHAPTER 5 SLEEP AND THE MCCOLLOUGH EFFECT

5.1. Introduction

In their experiments MacKay and MacKay (1974a, 1975a and 1977b) reported that when a night's sleep intervened in the course of measuring the decay of the McCollough effect, the measured strength on waking was equal to, or greater than, the reading before sleep (fig. 5.1). They further noted that after as many as 10 hrs. of sleep there was no significant decay in the measured strength of an OCCA, induced just before going to sleep (MacKay and MacKay, 1977b). In normal circumstances a 10 fold decay would have been expected for the same initial strength. The observation that the readings after sleep were often higher than the night before was confirmed in some preliminary experiments by the author.

Fig. 5.1. (MacKay and MacKay, 1975a)



Typical examples of time-course of McCollough effect over 2 days and nights [for same subject as in Fig. 2 on different occasions with initial exposures of 12 min (□) and 20 min (O)]. Note apparent arrest of decay overnight (arrows). Scales of time and strength are logarithmic.

During these experiments it was further noted that the initial strength of the McCollough effect induced after nights of poor sleep were usually lower than those induced following a normal night's sleep, even when identical induction conditions were used. It seemed possible that variation in the number of hours sleep was responsible for some of the variability of the McCollough effect. A number of experiments were performed to investigate this possibility.

5.2. Changing Sleep durations: bedtime variable, induction hour fixed

5.2.1. Introductory Experiments

There were a number of ways of varying sleep duration. In these introductory experiments subjects were asked to vary the number of hours sleep by changing the time of going to bed and waking at a fixed hour. Subjects were also requested to vary their sleep duration only after they had had a standard sleep on the previous night. The experiments were performed as far as possible at a standard hour each morning, a set interval after waking. This time and interval varied slightly between subjects, owing to various domestic factors, but was fixed for each subject. After the set interval, subjects spent 10 mins. in the laboratory, under standard illumination, before performing the pre-test. A McCollough effect was then induced by using a 15 min. period, comprising intervals of 1s 'on' and 4s 'off'. Subjects were asked to eat and drink the same breakfast before each experiment and to expose themselves, as far as possible, to the same visual stimulation. These external factors were recorded on a standard questionnaire, shown in table 5.1.

Table 5.1.

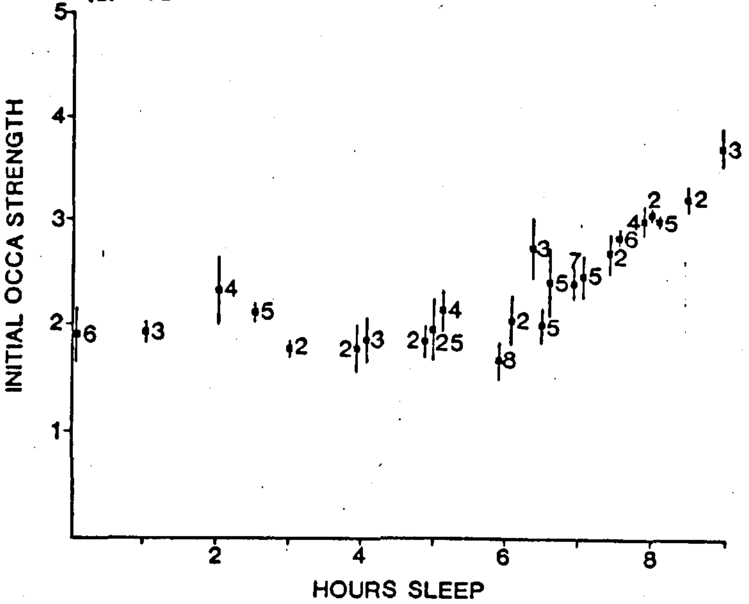
1. How many hours sleep did you have last night?
2.(a) How many hours sleep did you have the night before?
  (b) Is this about average?
3. How long have you been awake?
4.(a) Did you have a standard breakfast?
  (b) If not, how did it vary?
  (c) How many cups of coffee or tea have you had?
5.(a) Have you had any unusual visual stimulation?
  (b) If so, what was it?

Each experiment was performed at intervals of 2 days or more after the previous induction to allow the OCCA to decay. The duration of sleep was varied randomly. Outside of laboratory controlled experiments it is difficult to assess accurately the amount of sleep that subjects have had and these experiments have relied upon their own subjective assessment. A number of reports, however, have indicated that such assessments are reasonably accurate (Baekeland and Hoy, 1971). Assessment of the shorter periods of sleep were likely to be underestimated and long periods of sleep overestimated (Johns, 1977).

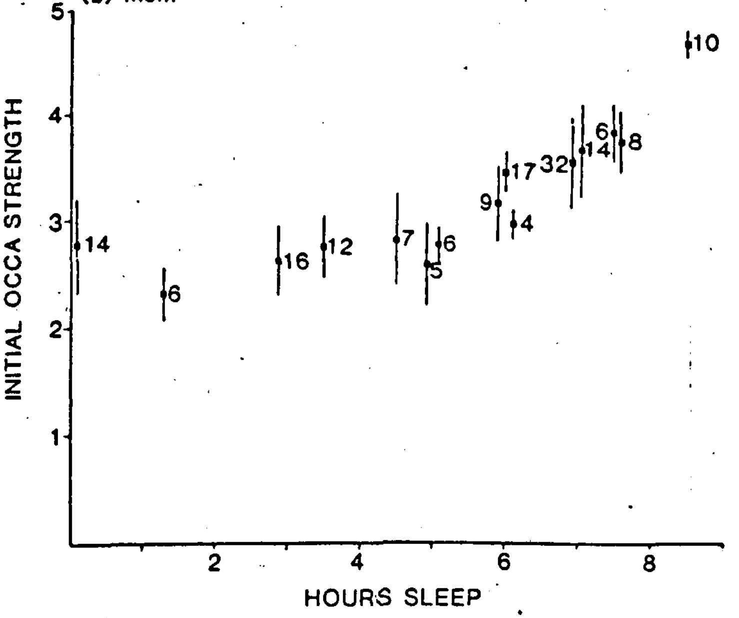
The McCollough effects were measured after a standard 1 min. rest period following induction. Pre-test readings were subtracted from this reading to give the initial strength. The results for one subject (NJL, Fig. 5.2a) show 24 runs spread over a period of several months. Periods of up to 5 hours sleep before the standard induction time made very little difference to the induced strength of the effect. For sleep periods from 5 to 9 hours, however, there

Fig. 5.2. Bedtime variable: induction hour fixed

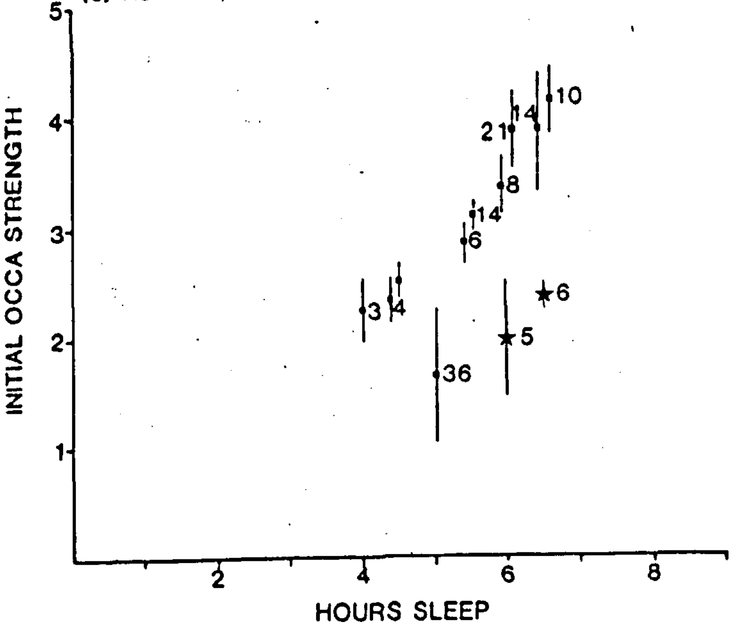
(a) NJL



(b) MJM



(c) RJW



was a strong positive correlation between sleep duration and the initial OCCA strength. The results for 2 other subjects (Fig. 5.2b and c) show similar trends. They indicate that sleep deprivation reduces the initial OCCA strength, for a standard stimulus sequence, to half or two thirds of the strength developed after a full night's sleep (about 7.5 to 8 hrs. for all these subjects). Sleep deprivation below a certain level causes no further decrease. Even after a totally sleepless night, the induced OCCA was still at baseline strength. There is a critical point which varies around 5 to 6 hrs. sleep, after which further sleep seems to boost the McCollough effect strength. One subject (RJW, Fig. 5.2c) was tested on two occasions, marked with stars, after suffering a week of repeated sleep deprivation. On these runs he failed to reach the expected OCCA levels. A number of spot checks were made upon subject NJL to investigate the effects of repeated sleep deprivation. On 3 occasions the McCollough effect was induced after 7hrs sleep following 3 nights of 5hrs sleep. The OCCA strength was found to be 2.0, 2.15, and 1.9 which compares with an average of 2.45 after standard runs (see Fig. 5.2a). This indicates that repeated sleep deprivation has a cumulative effect upon the strength of the aftereffect.

The figures next to each point represent the number of days since the last induction period. These show no correlation with the strength of the McCollough effect but provide evidence that any 'carry-over' between inductions was negligible and was not responsible for the trend that emerged.

5.2.2. Subjects with different sleep habits

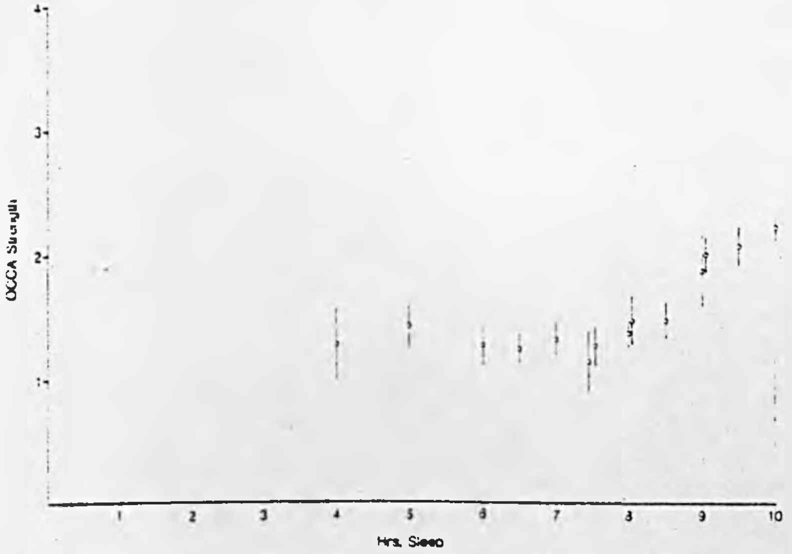
The trends shown by the 3 subjects in the introductory experiments were very similar. Both the start and the amount of the 'upturn' in the graphs were the same. Later experiments showed that this similarity was somewhat coincidental and may have been due to the similarity in the sleep habits of the 3 subjects. All these subjects habitually slept 7.5 to 8hrs from between 12am and 8am. This section reports the effect of changing the sleep duration of 2 subjects who usually slept 9 to 10hrs. The results for these subjects are shown in fig. 5.2d and e. They show, as with the others, an increase in the initial OCCA strength after longer sleep durations. In this case however the 'upturn' in the graph occurs after sleep durations of more than 7hrs and is not as large. It seems that differing sleep habits lead to slightly different trends. The results of section 5.2.1. are not, therefore, characteristic of all subjects and variation in sleep habits could be the source of some intersubject variability of the aftereffect.

5.2.3. Further Subjects

Owing to the demanding nature of the experiments, there was a lack of subjects who were willing to undertake a series of runs. There were, however, a number of people who were willing to do 2 or 3 runs. The experimental conditions and procedure were identical to those reported in section 5.2.1. The results for 7 subjects are shown on a composite graph (Fig. 5.3). Although these are too fragmentary to show detail they indicate that, in line with the trend shown in Fig. 5.2, longer periods of sleep are associated with an increase in the induced OCCA strength for all subjects.

Fig. 5.2

(a) SRD



(a) JCH

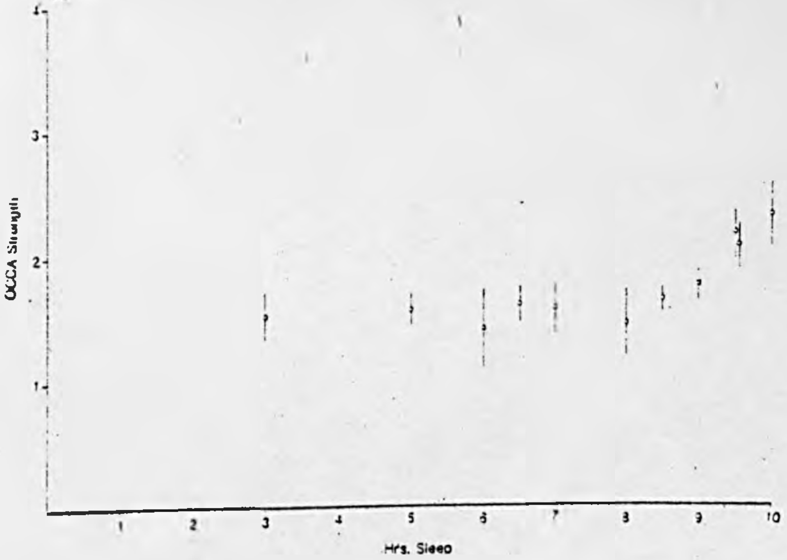


Fig. 5.3.

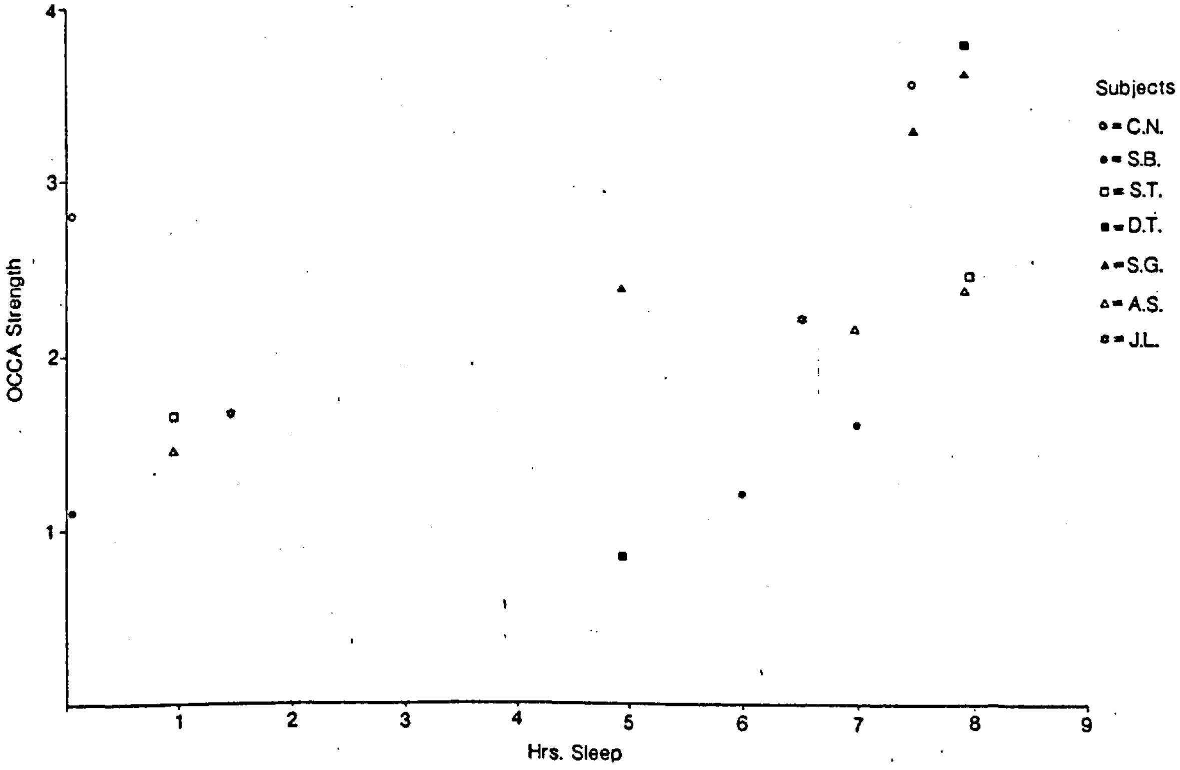
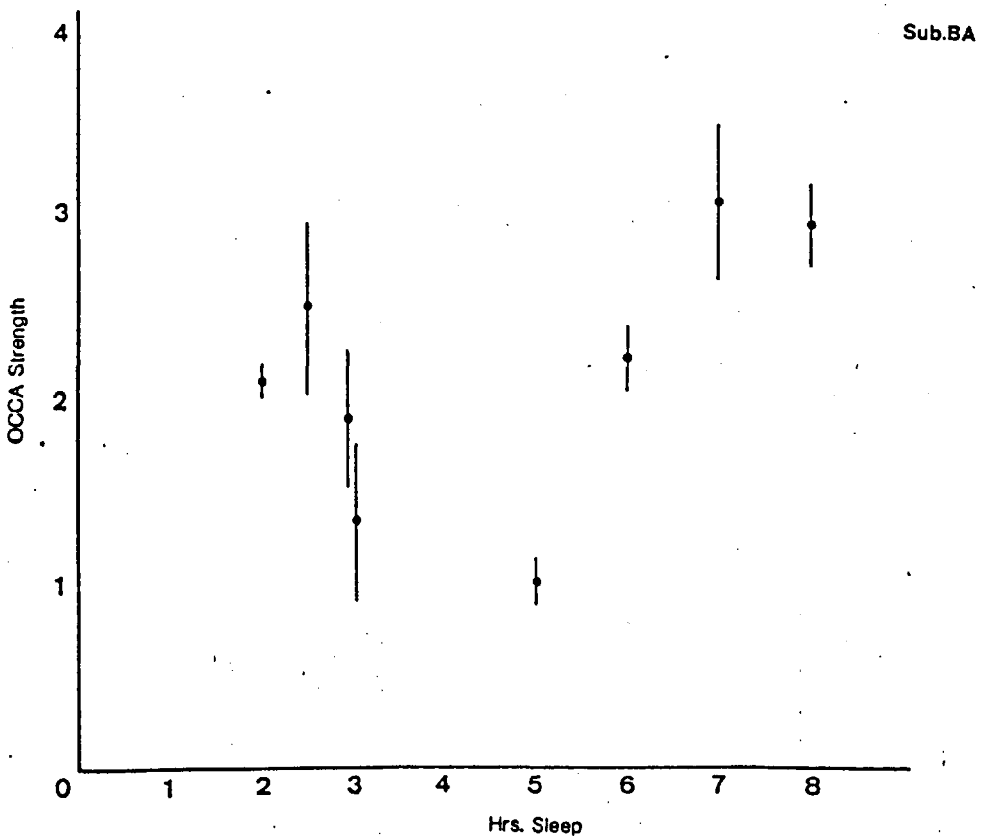

OCCA Strength
1
2
3
4
Hrs. Sleep
1
2
3
4
5
6
7
8
9
Subjects
○ = C.N.
● = S.B.
□ = S.T.
■ = D.T.
▲ = S.G.
△ = A.S.
● = J.L.

Fig. 5.4.


Sub.BA
OCCA Strength
0
1
2
3
4
Hrs. Sleep
1
2
3
4
5
6
7
8

5.2.4. Induction hour in the late afternoon

One subject was conveniently sleep-deprived at regular intervals, owing to the nature of his research. He performed physiological experiments throughout the night and slept in short bursts, usually amounting to 3 to 4 hours. Unfortunately, the McCollough effect could not be induced and recorded until about 5 or 6 pm, as his experiments continued throughout the day. The standard induction hour in these runs was, therefore, fixed at 6pm which was 12 to 13 hours after waking. In all other respects the experimental procedure was identical to that reported in section 5.2.1.

The results (Fig. 5.4) show the same trend as that shown in Fig. 5.2, but are more variable. It is not clear whether there is a 'baseline' level because the results for fewer than 6hrs. of sleep vary so much. In addition the standard error of each run is also very large. These variations may be due to a number of factors. The runs below 6hrs. of sleep were recorded after short bursts of sleep during the night, rather than after a continuous stretch. Agnew and Webb (1971) have reported that some subjects lack the ability to discriminate brief periods of sleep from wakefulness. Furthermore, since these runs were conducted 12 to 13 hours after waking, rather than 1/2 to 1 hour, it was impossible to have the same level of standardization of diet and visual stimulation as in the other subjects. For example, one possible factor, coffee intake, varied between 5 and 14 cups. It has been reported that caffeine, an active ingredient of coffee, influences the strength and decay of the McCollough effect (Shute, 1978). There was variation in both the type and amounts of other parts of the diet.

5.2.5. Effects of prior sleep on decay

The results have shown that changes in the prior sleep duration, or pattern, influence the initial strength of the McCollough effect. Since it is known that the decay of the McCollough effect is arrested by a period of sleep (MacKay and MacKay, 1974a, 1975a and 1977b), it was decided to investigate the effect of prior sleep duration upon the decay rate. Shute (1978) has reported that after sleep deprivation, the McCollough effect in one subject showed little or no decay. From this one might expect that the large OCCA observed after a good night's sleep would decay at a faster rate than the small effect observed after sleep deprivation.

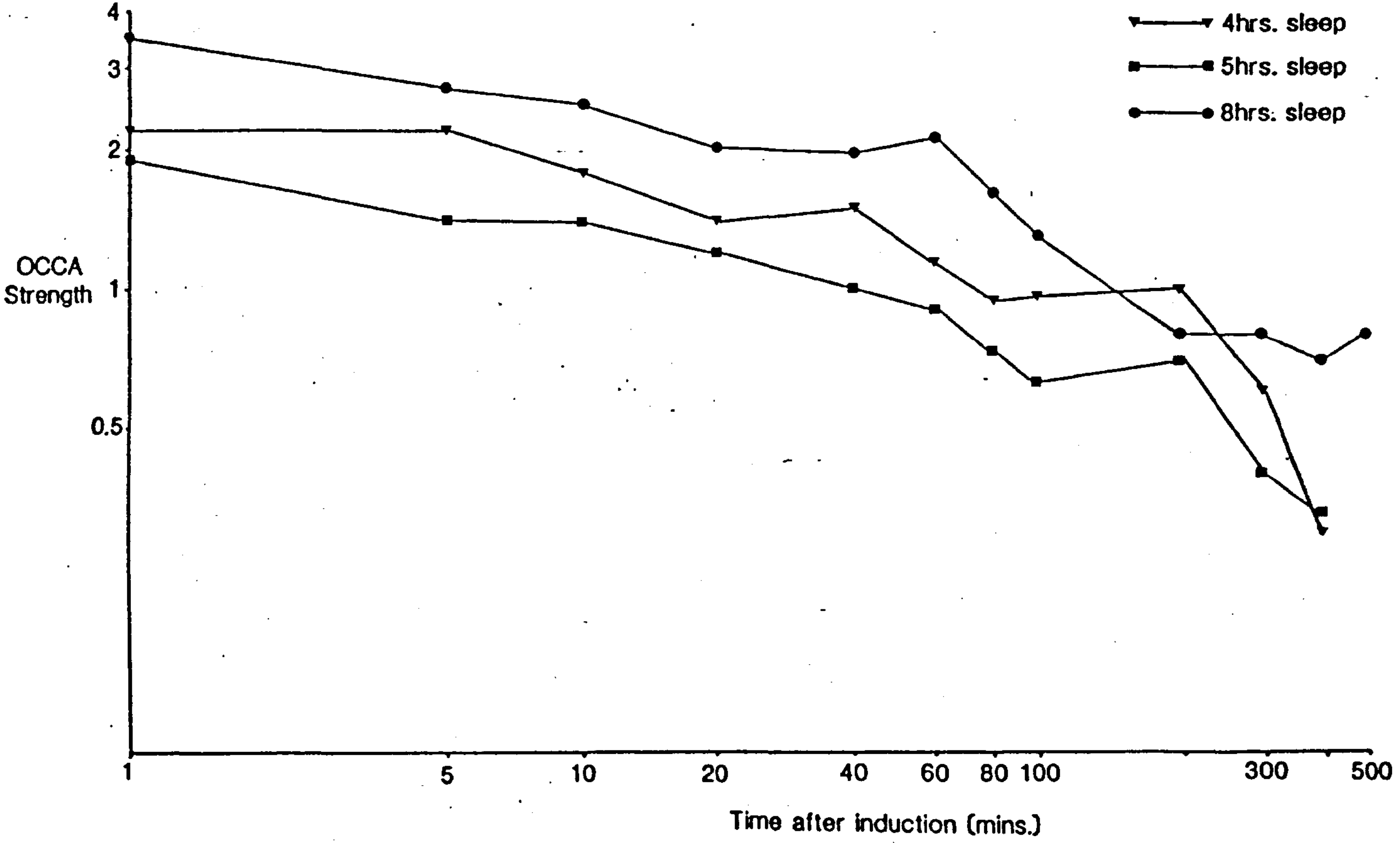
The decay rate of the McCollough effect was recorded following a number of the runs reported in section 5.2.1. Decays were measured after having 4,5 or 8 hours sleep as the initial strength varies significantly after different sleep durations. The results shown in Fig. 5.5 indicate that, although the initial strength varies significantly, the decay slopes (on log-log plots) do not.

5.2.6. Conclusions

The results show that the duration of sleep before a standard induction strongly influences the initial strength of the McCollough effect but has no measurable effect on the decay rate. The effect of prior sleep upon the strength of the McCollough effect may be due to a number of factors:

1. The amount of sleep.
2. As the bedtime was variable, the effect recorded at a fixed

Fig. 5.5. Effects of prior sleep durations on decay rates



hour in the morning may result from a disruption of a circadian change, which occurs at a critical period during the previous evening.

3. The OCCA may be reduced by the extra visual stimulation received during the increase in waking hours.

4. The alertness and ability of the subject may be decreased owing to the lack of sleep.

A number of experiments were performed in an attempt to isolate the factor responsible.

5.3 Subject alertness and ability

One possible explanation of the results reported in section 5.2 is that sleep deprivation affects the subject's alertness and ability. Both animal and human data have shown that sleep deprivation affects psychological ability. Prior REM (rapid eye movement) sleep deprivation has been shown to impair discrimination-learning in rats (Pearlman and Becker, 1973) and mice (Fishbein, 1971). REM sleep deprivation, prior to training, impairs the formation of a permanent memory trace in man (Fishbein and Gutwein, 1977). Tilley and Empson (1978) and Fowler, Sullivan and Ekstrand (1972) have shown that REM sleep facilitates memory consolidation. These results may be relevent to the trend observed in section 5.2, as REM sleep is known to increase in the last third of a normal night's sleep (Warburton, 1975) or after the first 3hrs of sleep (Williams, Agnew and Webb, 1964). Sleep deprivation is known to reduce attentional control (Hockey, 1970; Fisher, 1980). Wilkinson (1968) showed that performance on vigilance tests was impaired when sleep was reduced to 2hrs. or less and that false reports increased below 3hrs. sleep. He also reported that below 3hrs. sleep, subjects' 'intrinsic capacity' to discriminate signals, and their willingness to report signal detections, decreased. The runs reported in this chapter lasted approximately 25 minutes. Wilkinson (1961) has shown that sleep deprivation has little effect upon short tasks (5mins or less) but does affect subjects' ability to perform longer tasks (over 15mins). Wilkinson, Edwards and Hains (1966) have reported that 7-5hrs sleep on a single night had little effect upon the the vigilance of subjects but between 5 and 3hrs there was a steep decline in vigilance ability. Less than 3hrs caused no further decline. The trend observed in section 5.2. may therefore be due to sleep deprivation which affects the subject's ability to perform the colour match, or his ability to concentrate upon the induction patterns. Subjects reported that sleep deprivation does not seem to affect their ability or concentration. Two tests were performed during random runs to give an objective measure of their ability to perform the experiments.

1. The variability of the pre-test was recorded.
2. A contrast measurement was taken.

5.3.1. Pre-test Variability

The variability of the pre-test recordings was examined to assess the ability of the subject to perform the colour match. Since the pre-test measurements are performed with little or no colour bias, the subject should have about the same value and variability on each occasion, unless sleep deprivation impairs his ability. Table 5.2 shows the mean and the standard error of the pre-test readings of 3 subjects after different amounts of sleep.

Table 5.2.

SUBJECTS	NJL		MJM		RJW	
HOURS SLEEP	MEAN	S.E.	MEAN	S.E.	MEAN	S.E.
3	0.3	0.1	0.15	0.2	0.4	0.2
4	0.1	0.1	0.4	0.13	0.4	0.2
5	0.2	0.15	0.2	0.1	0.3	0.15
6	-0.1	0.3	0.3	0.05	0.3	0.12
7	0.25	0.05	0.0	0.07	0.25	0.17
8	0.2	0.13	0.2	0.17	0.35	0.14

The table shows that the pre-test variability does not vary consistently with the number of hours sleep. Fig. 5.2 also shows that, although there is some fluctuation in the standard error of the results, the variation does not correlate with the amount of sleep.

5.3.2. Contrast Measurement

A subject's ability to concentrate on gratings was assessed before a number of runs by recording the luminance at which they could no longer perceive a fine grating (18 cycles per degree). The grating was placed in an apparatus in which the luminance could be varied. The luminance at which the grating could just be seen was recorded. Six readings were taken before the pre-test procedure: 3 as the luminance was lowered and 3 as it was increased. A smooth knob varied the luminance of the grating and the amount by which it was turned could be read to 2 degrees. It was found that the photometer could not accurately distinguish the luminance change caused by 8 degrees of turn of the knob and the results (Table 5.3.)

have therefore been presented as the mean angle through which the knob was turned from zero.

Table 5.3.

SUBJECTS	BA	NJL	MJM
HOURS SLEEP	MEAN	MEAN	MEAN
3	136	138	139
4	134	140	135
5	135	136	139
6	138	136	135
7	137	141	138
8	133	137	136

They show that both the mean and standard error of the readings do not vary consistently with the number of hours sleep.

5.3.3. Conclusion

The subject's ability to perform colour matches and to concentrate upon gratings does not seem to be impaired by sleep deprivation. The results reported in section 5.2, therefore, are not due to reduction in the subject's ability or concentration. Moreover one would expect that if reduction in the strength of the OCCA were due to impairment of ability, the decrease would continue with increased sleep deprivation and be maximum at Ohrs. The results show no further decrease of the McCollough effect strength after 3 to 4hrs sleep deprivation. Finally, one might argue that sleep deprivation in some way reduces the saccadic eye movements of the subjects and thus reduces the strength of the McCollough effect since it has been shown that lack of eye movements, or stabilised vision during induction results in no OCCA (Piggins and Leppmann, 1973). This argument may be countered by the observation that during all the experiments reported here subjects constantly moved the direction of their gaze around a circle on the induction patterns to stop any fixation.

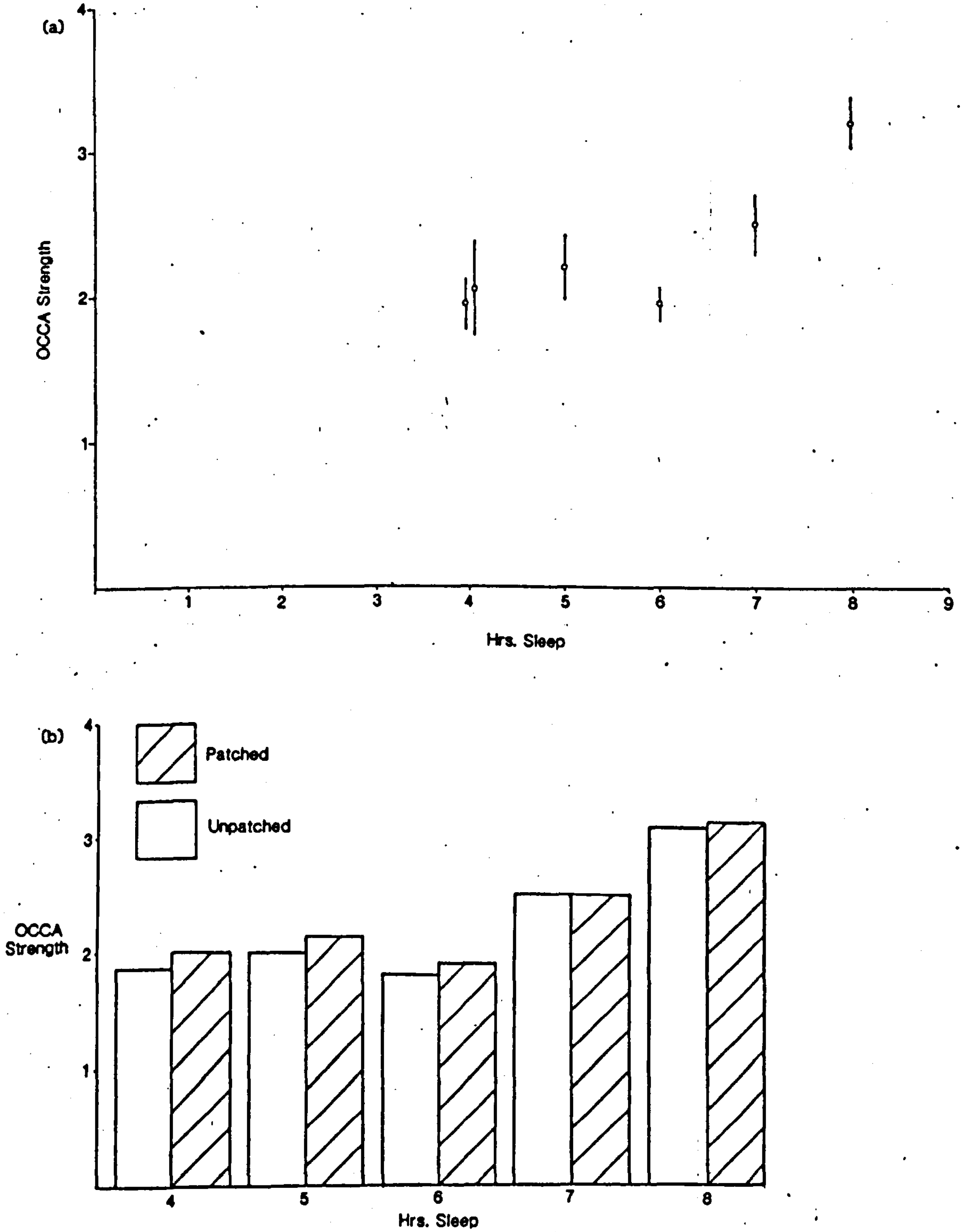
5.4. Effects of Darkness

It has been demonstrated by MacKay and MacKay (1975a, 1977b) that keeping an eye in darkness has the same effect as sleep upon the decay of the McCollough effect. They found that if one eye is totally occluded after equal effects are induced in both eyes, it retains the effect at full strength. The effect in the unoccluded eye, however, decays as a negative power function of time. When the occluded eye is exposed its OCCA begins to decay at the same rate.

5.4.1. Patching one eye for 5hrs. before sleep

One explanation of the results of section 5.2 could be that a lower McCollough effect is induced after short periods of sleep because of the extra exposure to light on the previous evening. This possibility was investigated by wearing a light-tight eye patch over one eye for 5 hours, prior to sleep. In all other respects the experimental procedure was identical. Subjects varied the number of hours sleep by varying their bedtime and waking at a set hour. The results (Fig. 5.6a) show the same trend as, and are approximately the same values as the results shown in Fig 5.1a. Fig. 5.6b shows a bar graph of the occluded and unoccluded eye readings after various sleep durations. Although the readings are not identical they do not differ significantly, or in a consistent manner. The results

Fig. 5.6. Effects of keeping eye in darkness for 5 hrs before sleep



indicate that patching an eye before sleep has no effect upon the strength of the McCollough effect induced after waking.

5.4.2. Effects of patching one eye while sleeping

The possibility that extra light stimulation causes a reduction in the McCollough effect was further investigated by occluding one eye with a light-tight patch while sleeping. The subject slept in a brightly lit room, of average luminance of 8mlm, so that one eye was deprived of light and the other received some stimulation all night through the eyelid. The results for the two eyes after varying amounts of sleep are shown in Table 5.4.

Table 5.4.

HOURS SLEEP	OCCLUDED EYE	UNOCCLUDED EYE
5	1.95	2.05
6	2.15	2.10
7	2.80	2.85
8	2.95	2.90

The results indicate that the effect of total light deprivation is not consistently different from partial light deprivation. Increasing sleep again shows a consistent increase in the OCCA strength.

5.4.3. Conclusion

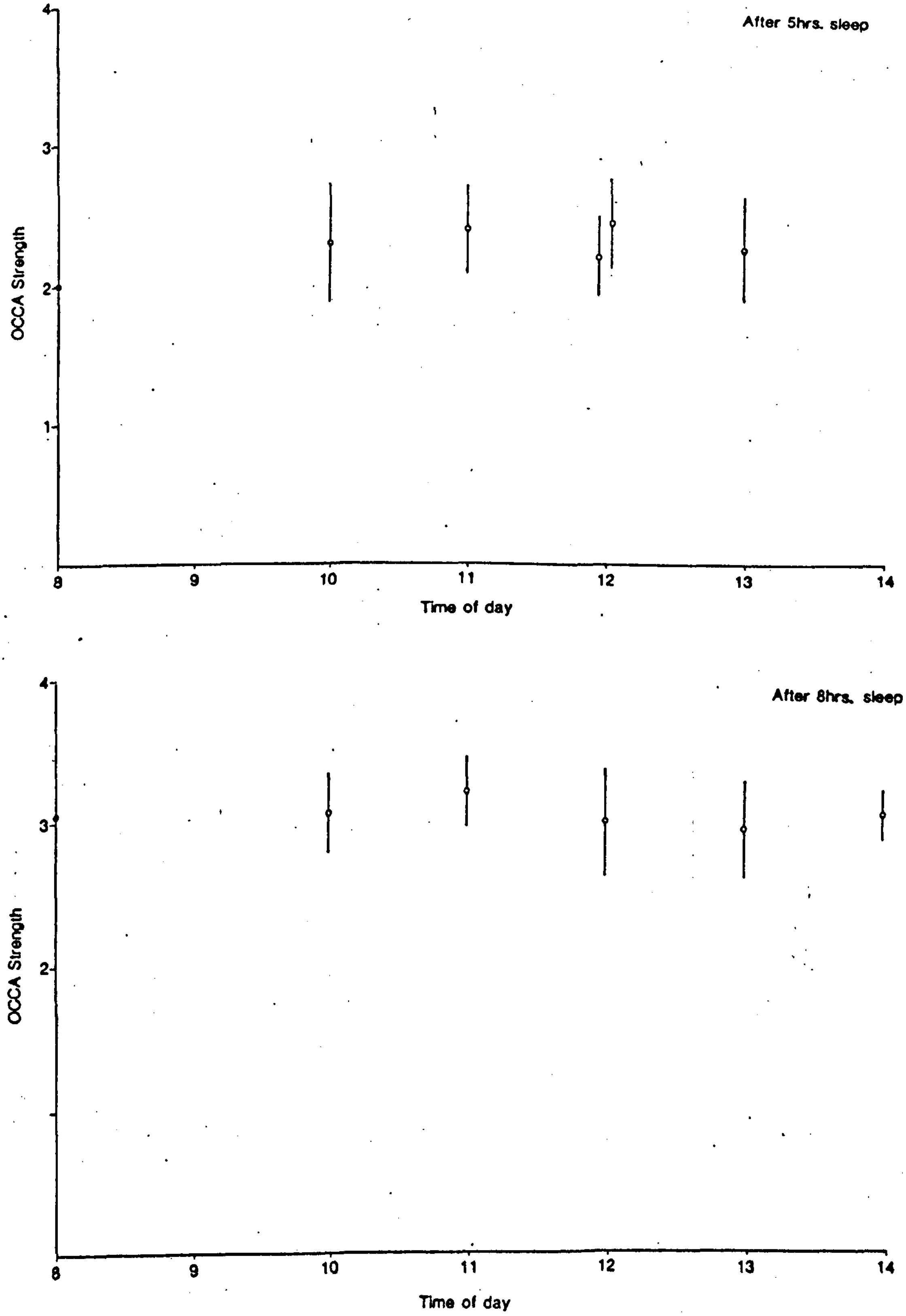
The results show that the decrease in McCollough effect strength obtained after short periods of sleep is not caused by the increase in light stimulation on the previous evening. Although sleep and darkness both allow the effect to be retained when they interrupt a period of decay, darkness prior to induction has no effect.

5.5. Effects of patching in the morning

In this experiment a light-tight patch was worn over one eye for various periods after waking, to determine the effect of darkness upon the McCollough effect later in the morning. The hypothesis being tested was that the variation in the strength of the OCCA observed on waking was a transitory effect which would fade during the day as a result of visual stimulation. To vary the sleep duration, bedtime was varied and the waking time was fixed at 8am. No food or coffee was consumed before the induction period (because of the variation in the period between waking and induction). Patches were worn for up to 6hrs after waking. Fig. 5.7 shows the effect of wearing a patch after sleep lasting 8hrs and 5hrs for between 0 and 6hrs after waking. The induction was performed 10mins. after the removal of the patch, to allow the dark adapted eye to recover.

These results show that patching an eye after sleep does not increase or decrease the initial strength of the McCollough effect but that the prior sleep duration is correlated with the strength.

Fig. 5.7. Effect of keeping eye in darkness after waking



They also indicate that the trend shown in Fig. 5.2 is not transitory, but is evident at least 6 hrs. after waking in either darkness or normal visual stimulation.

5.6. Bedtime fixed, induction hour variable

All the experiments described in the previous sections have changed the number of hours sleep by varying the bedtime and waking at a set hour. The results obtained could therefore be due not to the amount of sleep but to the timing of the sleep or the increase in waking hours at night. It is known that sleep has different effects on memory when it occurs in different halves of the night (Yaroush, Sullivan and Ekstrand, 1970). The increase in waking hours might conceivably affect some internal circadian rhythm during a critical period. The latter hypothesis could explain why the strength of the McCollough effect on waking increases after 5 to 6hrs. sleep but remains stable for sleep durations between 0 and 5hrs. The critical period in the experiments reported would then be from 11pm to 3am. It was decided to test this possibility by changing the method of varying the sleep duration. The number of hours sleep was altered by varying the waking time and keeping the bedtime fixed at 11pm. Experimental runs were performed only after nights when the subject had gone to sleep within 15 mins of going to bed. There was no independent measure of the time between going to bed and going to sleep (the sleep latency) but Johns (1977) has shown that subjective reports are 'valid as well as reasonably reliable and accurate'. Induction periods were as in the previous experiments, performed following a set interval after waking and the subject's diet and intervening visual stimulation were kept as constant as possible.

The results (Fig. 5.8) show the same trend and are approximately the same values as the results for the same subject shown in Fig. 5.2a. The strength of the McCollough effect remains below 2.0 for sleep durations from 0 to 5-6hrs and then rises with further increase in sleep duration.

Conclusion

The results indicate that the strength of the McCollough effect, when induced on waking, is affected by the number of hours of prior sleep, but that the timing of the sleep has no significant effect. The trend observed in the original experiments was not therefore due to a disruption of some circadian rhythm during the previous night.

5.7. Bedtime fixed, induction hour fixed; sleep variable

Although the experiment reported in section 5.6 showed that the results are not due to a disruption of a circadian rhythm before sleep, it was possible that the trend observed could be due to internal physiological changes during the morning. The induction hour varied between 2.30am and 8.30am because of the changes in sleep duration. The possibility that the variation in the induction hour was responsible for the trend observed was tested by repeating the experimental procedure of section 5.6 but with the induction hour fixed at 8.30am. Intervals between waking and induction therefore increased with a decrease in sleep duration.

Fig. 5.8. Bedtime fixed: induction hour variable

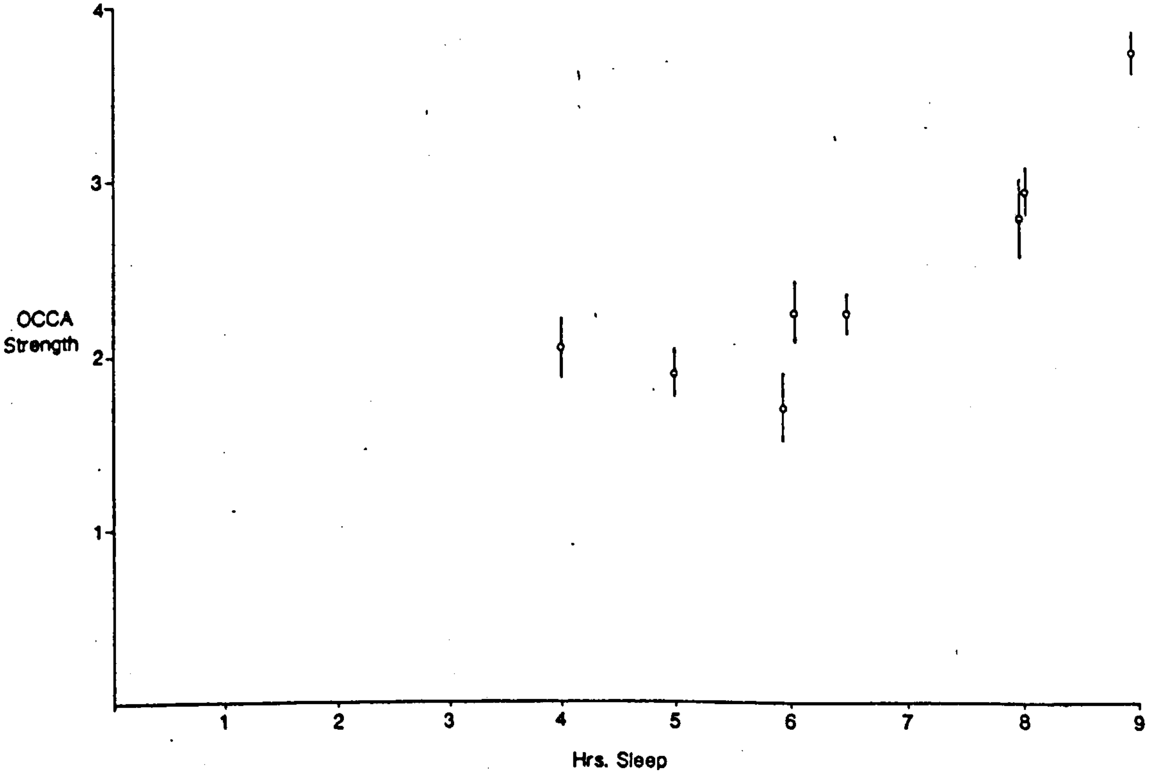
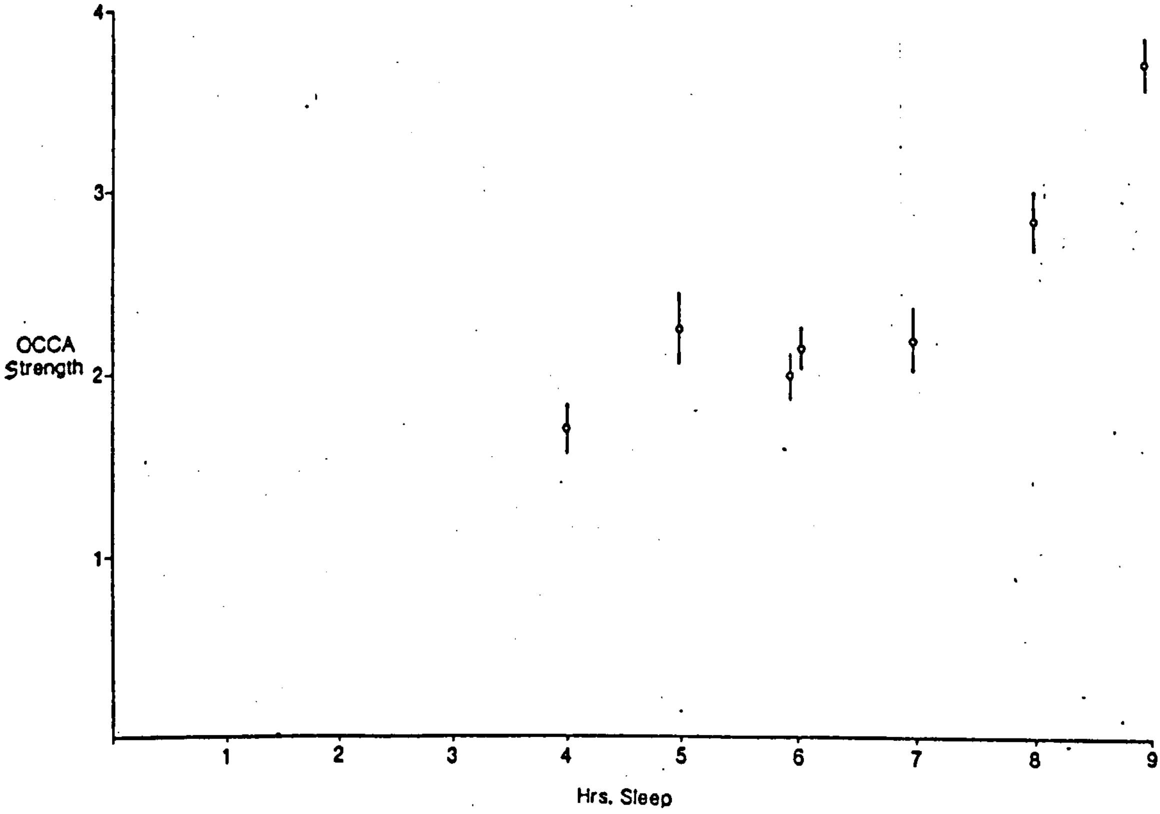


Fig. 5.9. Bedtime & induction hour fixed: sleep duration variable



Again the results (Fig. 5.9) show the same trend as Fig. 5.2a. An 'upturn' in the graph does not occur until 7hrs sleep but this may reflect one aberrant result (at 7hrs sleep). The rest of the results do not vary significantly from those obtained on Fig. 5.2a.

Conclusion

The results obtained in section 5.6. are not due to the variation in the induction hour. The trends that emerged seem to be due to the sleep duration.

5.8. Bedtime variable, induction hour fixed; 2hr. shift in prior sleep cycle

The possibility that the reduction of the initial McCollough effect strength after reduced sleep results from a disruption of a circadian rhythm was further investigated by shifting the sleep cycle. The sleep pattern of one subject (NJL) was shifted by 2hours from 12pm-8am to 2am-10am. McCollough effect strengths were then recorded, over a period of 2 weeks, after various sleep durations. Change in the sleep duration was again produced by keeping the waking hour fixed and changing the bedtime.

The results (Fig. 5.10.) show a similar trend and yielded approximately the same values as those presented in Fig. 5.2a. They indicate that a disruption of the circadian rhythm, after shifting the sleep cycle, has little effect upon the inital McCollough effect strength, whereas changes in sleep duration have a strong influence.

Fig. 5.10. Bedtime variable: induction hour fixed: 2hr shift in prior sleep cycle

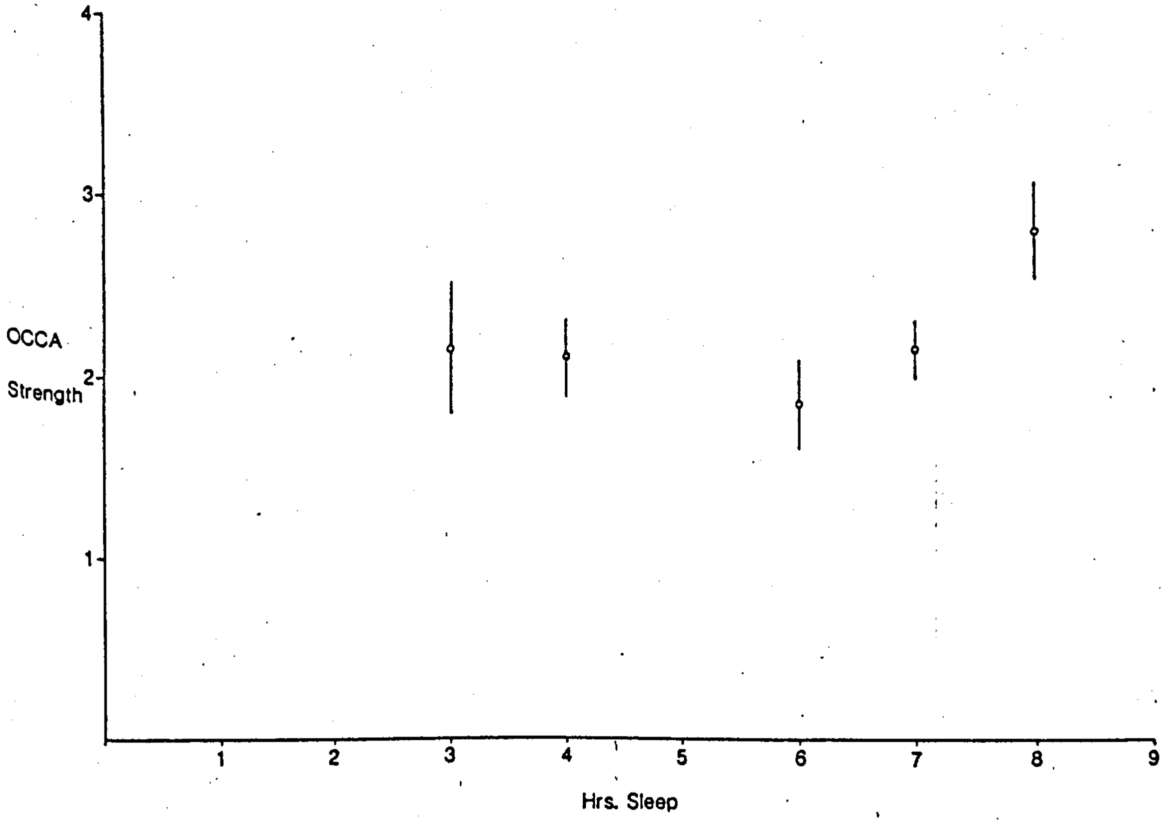
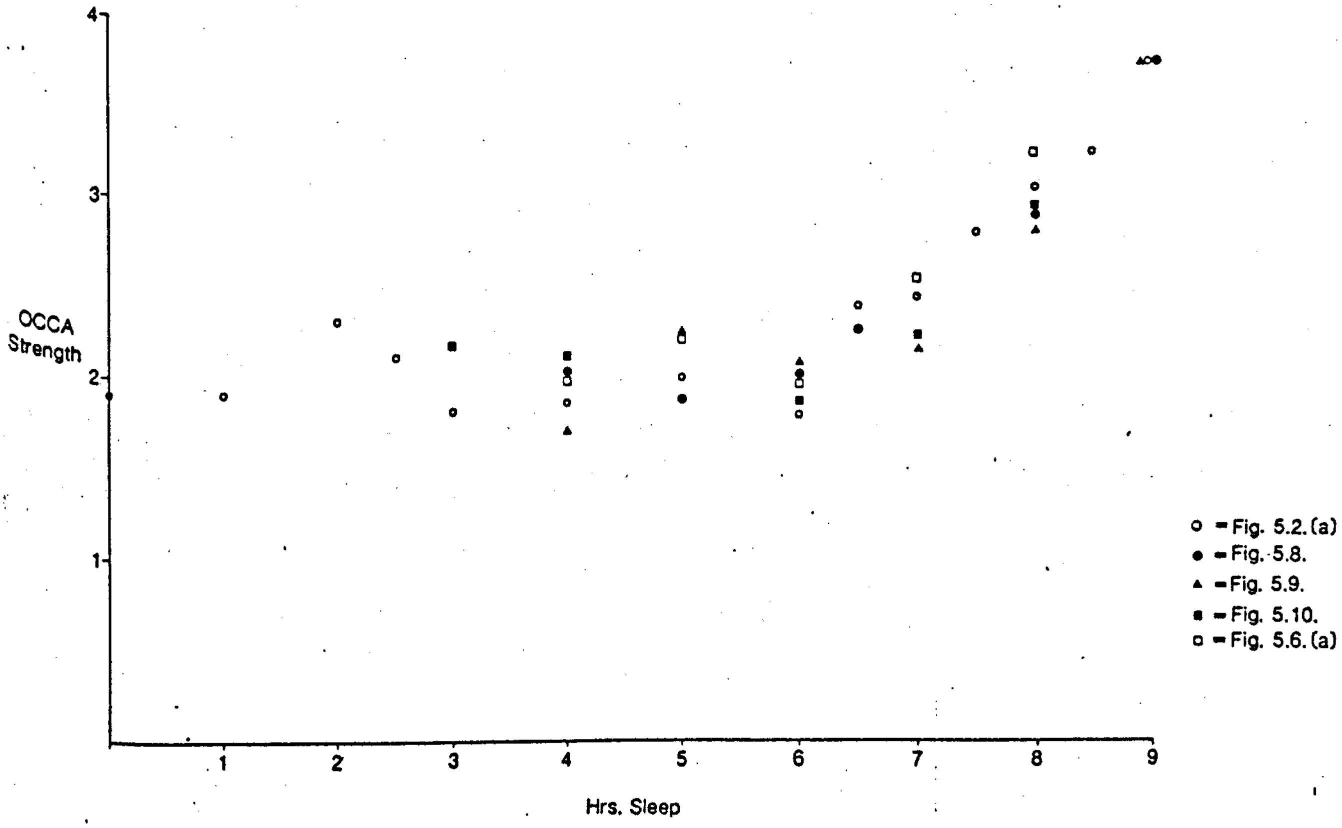


Fig. 5.11. Summary of results



5.9. Conclusions and Discussion

The results of this chapter have shown that the strength of the McCollough effect is strongly influenced by prior sleep duration. Aftereffects induced after 0-5hrs sleep were low in strength but when the sleep duration was lengthened from 5 to 9hrs, the strength of the OCCA increased. This trend was independent of the number of hours in darkness and the timing of the sleep. Experiments also showed that the results were not due to a reduction in performance or to a lack of concentration. Sleep duration did not affect the decay rate of the aftereffect. Some of the results are summarized in fig. 5.11.

There are few reports of the effect of a few hours of sleep deprivation on visual perception. Those which do show a positive result have been recorded after sleep deprivation lasting 30hrs. or more. For example, Clark and Warren (1939) have shown pronounced changes in myopia, hyperopia and accommodation after 30hrs. sleep deprivation. They also showed a slight decrease in visual acuity and visual fields for four colours, but in common with other observers they noted that test results do not reflect the subjective mis-perceptions and visual hallucinations reported by most subjects (see for example Cappon and Banks, 1960; Pasnau, Naitoh, Stier and Kohlar, 1968). Most other links between vision and sleep have concentrated upon the effects of prior visual input on the length and types of sleep (Allen, Oswald, Lewis and Tagney, 1972; Bowe-Anders, Herman and Roffwarg, 1974; Horne, 1976).

It may be significant that the pattern of results which is most similar to that presented in this chapter, is to be found in reports upon the effect of sleep on memory and learning. It has been suggested that the McCollough effect probably results from some form of synaptic association (Creutzfeldt, 1973; MacKay and MacKay, 1975b). Although the McCollough effect consists of colours which are complementary to those originally presented, it is similar to memory processes in that it is retained until it is overwritten or decays. Most studies of sleep deprivation suggest that learning and memory are impaired during or just after the deprivation period (Williams Gieseling and Lutin, 1966). Recent evidence indicates that, although in general sleep facilitates memory (Jenkins and Dallenbach, 1924), retention is poor if a short period of sleep occurs just prior to learning (Ekstrand, Barrett, West and Maier, 1977). Sleep durations of between 0.5 and 4hrs result in a reduction in memory as compared with a control condition of no sleep. This effect fades when the sleep duration increases to 6hrs. These results suggest that the processes occurring during the early stages of sleep produce unfavourable conditions for the storage of new information and such processes may affect associative visual information processing.

Some studies have concentrated on specific stages of sleep. For example, many investigators have concluded that loss of REM sleep results in a decrement in memory (Fishbein, 1970; Fishbein and Gutwein, 1977; Pearlman and Greenberg, 1973; Tilley and Empson, 1978). The results of this chapter have shown that the loss of the last third of a normal nights sleep strongly affects the strength of subsequent aftereffects. This trend may be linked to the observation that most REM sleep normally occurs during the last 3hrs (Williams, Agnew and Webb, 1964) or the last third of sleep (Warburton, 1975). However, links between REM sleep and the

McCollough effect must remain speculative until the aftereffect is studied in conjunction with EEG controls.

There is a large body of evidence which shows that the electrical, metabolic and neurotransmitter activity of the brain changes during sleep and sleep deprivation (Jouvet, 1969; Jouvet, 1972; Fishbein and Gutwein, 1977). Total sleep deprivation causes a fall in the level of acetylcholine (Bowes, Hartman and Freedman, 1966) and of noradrenaline and serotonin (Tsuchiya, Toru and Kobayashi, 1969). After sleep deprivation, however, the level of serotonin rapidly rises to above control level (Toru, Shibuya and Shimazono, 1975). REM sleep deprivation appears to have different effects since Hery et. al. (1970) have shown that it causes an increase in the level of serotonin. After REM sleep there is an increase in the level of noradrenaline (Pujol, Jouvet and Glowinski, (1967). Satinoff, Drucker-Colin and Hernandez-Peon (1971) have demonstrated that REM sleep deprivation leads to paleocortical excitability and to an increase in the inhibition responsible for sensory filtering. Some of these changes in brain activity during sleep deprivation are concomitant with changes in memory (Fishbein, and Gutwein 1977; Wietzman, 1977). Moruzzi (1966) has suggested that one function of sleep is to allow some areas of the brain to recover from 'plastic' activities. Short periods of sleep would reduce the recovery period and therefore reduce the plastic abilities of the brain. It is possible that the changes in the strength of the McCollough effect after different sleep durations, are due to the differences in prior brain activity, during either the sleep deprivation or during the different sleep durations.

Whatever the mechanism responsible for the trend that emerged in this chapter, it is evident that changes in individual sleep habits may be significantly responsible for some intrasubject variability and that differences in sleep patterns could result in intersubject variability of the initially induced strength of the McCollough effect.

CHAPTER 6. TIME OF DAY AND THE MCCOLLOUGH EFFECT

6.1. Introduction

The experiments reported in Chapter 5 indicated that, although prior sleep duration had an effect on the initial strength of the McCollough effect, the timing of the sleep period had no effect. This was taken as evidence that there was no circadian rhythm influence upon the OCCA. However, during some exploratory experiments it was found that the McCollough effect did vary, apparently systematically, when induced at different times during the day. Dr. V.MacKay (personal communication) has reported that she tried to induce aftereffects at the same hour for any set of experiments because she suspected that there was a systematic change in the characteristics of the OCCA throughout the day. She has reported that the decay rate decreases when the induction period occurs later in the day (MacKay, 1978). This chapter reports some of the results of varying the induction hour of the McCollough effect. For clarity, the time of day will be based on a 24hr. clock system.

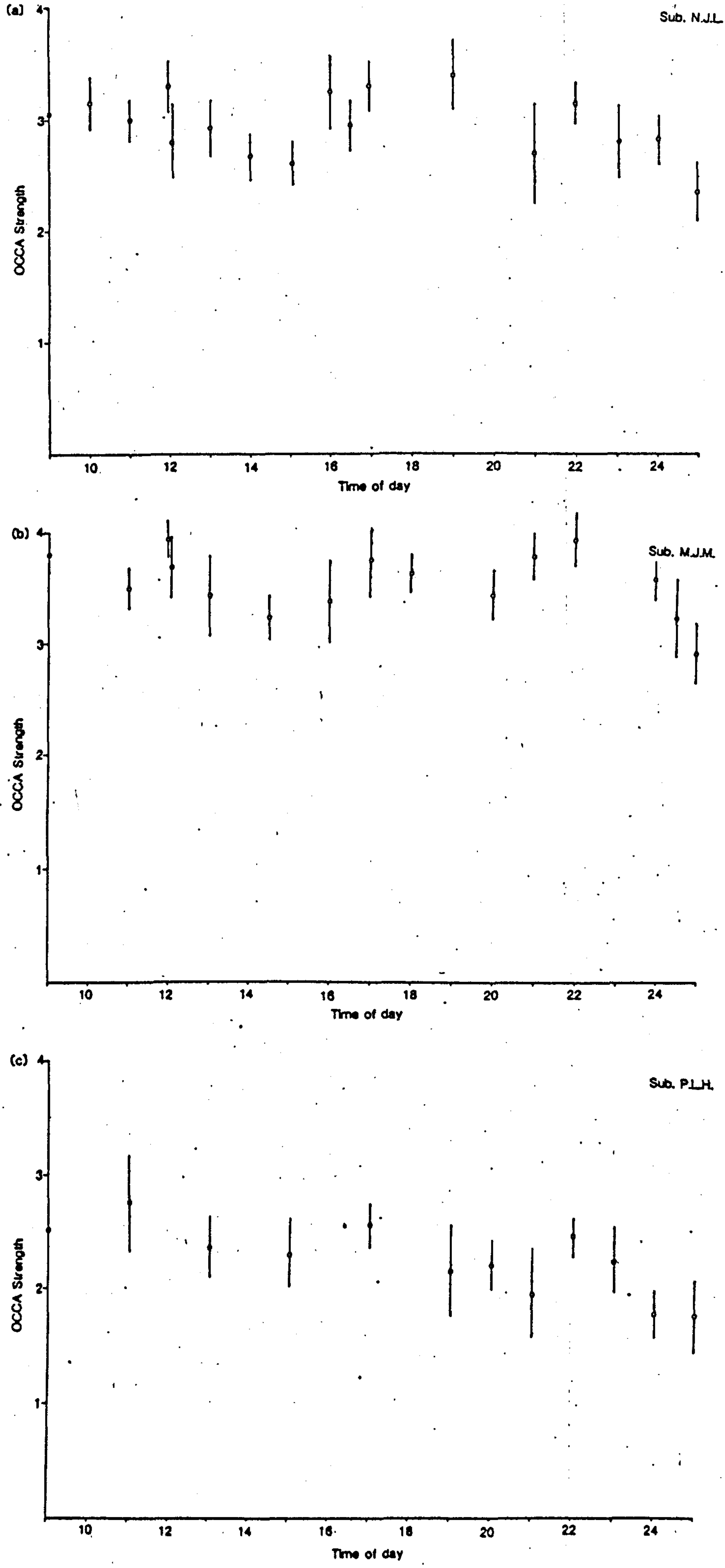
6.2. Variation of OCCA strength thoughout the day

Although the author's exploratory experiments had revealed some variations in the OCCA strength throughout the day, they had not been performed under standard conditions. McCollough effects were, therefore, induced at different hours after controlling as many factors as possible. A standard induction period of 15mins., consisting of 1s. 'on' and 4s. 'off' intervals, was used at different times of the day between the hours of 09.00 and 01.00.

The experiments were performed after a standard sleep the previous night for each subject. Both the bedtime and the waking time were fixed. Subjects spent 15mins. in the laboratory before each induction period under standard illumination. It was impossible to control the diet of each subject before each run since the induction periods occurred at different times of the day. Subjects were, however, asked not to smoke or consume anything for an hour before each experiment began.

The results for 3 subjects (Fig. 6.1) show that there is a considerable variation (up to 20%) of the McCollough effect during the hours studied. This variation appears to be largely random and may be due to changes in external factors, such as diet or the visual stimulation, before each run at a different hour. Two of the subjects appear to have a lower McCollough effect in the early afternoon than the late morning and late afternoon but this change is not significant. This drop may be due to the lunch the subjects usually ate, or to the fact that they ate outside the building and spent some time in increased illumination. Some experiments have shown that there is a consistant 'post-lunch' dip on a variety of human performance tests (Blake, 1967). This post-lunch dip was independent of the timing of mealtimes (Colquhoun,1971; Blake,1967). However, the post-lunch dip observed in the McCollough effect was not consistant. Despite the random in OCCA strength during most of the day, there does seem to be a systematic drop after 23.00 for each subject. Although the results after 23.00 are still variable, they do show a trend towards a lower OCCA and the results recorded at 01.00 are all lower than the results recorded throughout the rest of the day.

Fig. 6.1. Effect of varying induction hour



6.3. Induction in the evening

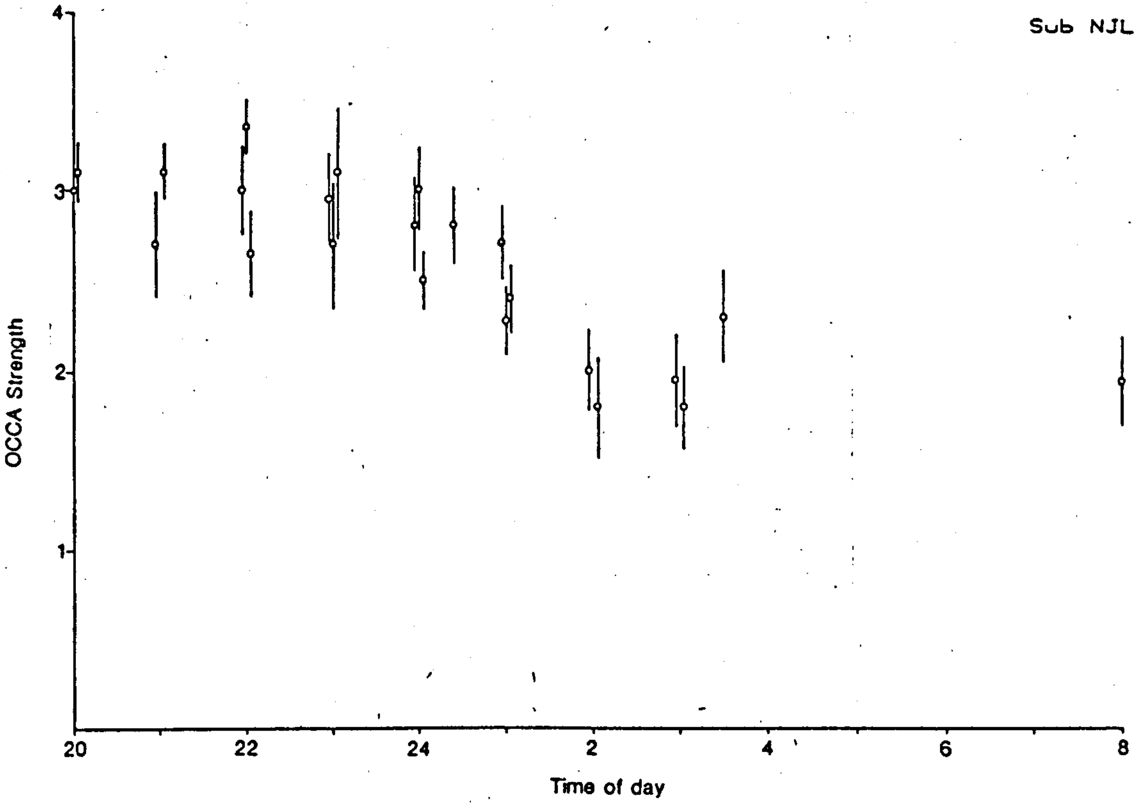
In view of the results obtained in section 6.2 it was decided to concentrate on the variation of the McCollough effect in the evening and early morning following a standard induction.

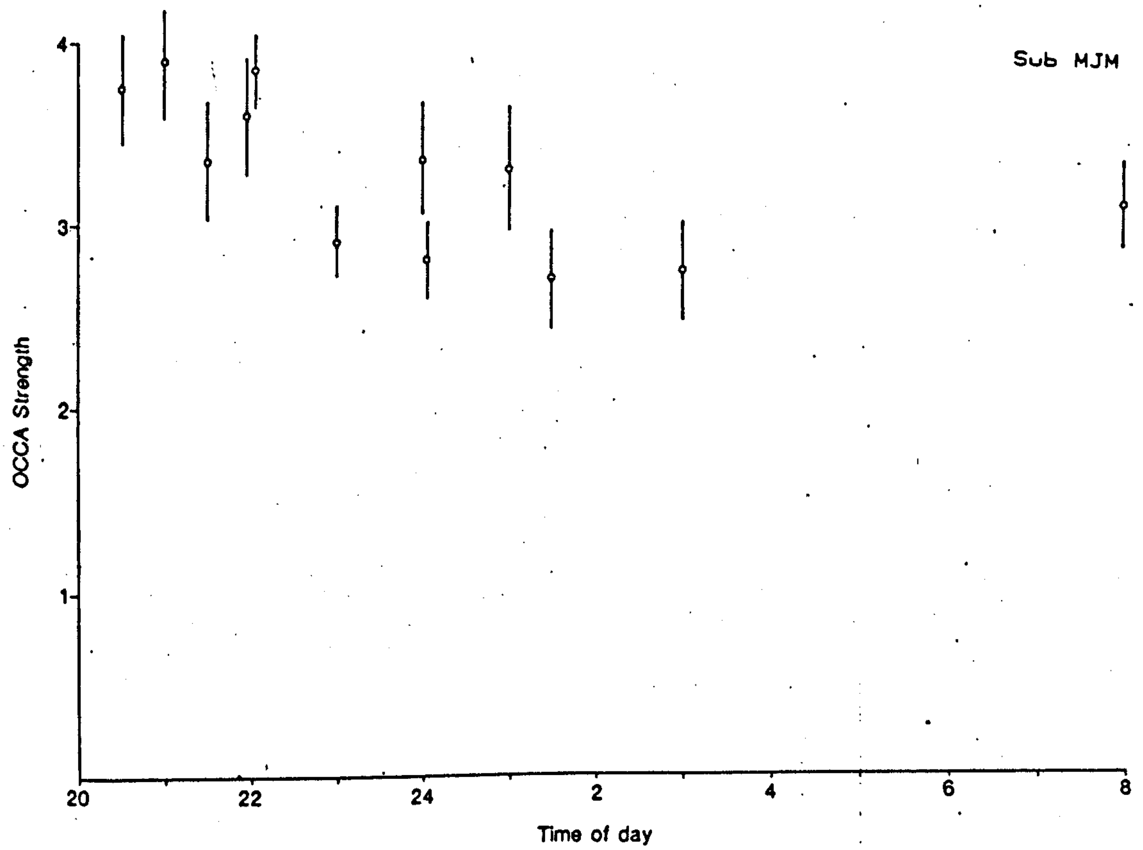
6.3.1. Initial OCCA strength

McCollough effects were recorded under standard conditions from between 20.00 and 08.00 and some runs, therefore, involved sleep deprivation. Nothing was consumed for 2 hours, rather than 1 hour, before these runs, in the hope that this would reduce the variability of the results. The standard sleep period before each run was from 00.00 and 08.00 for one subject (NJL) and 00.30 to 08.00 for the other (MJM).

The results of the two subjects (Fig. 6.2) show a systematic drop from approximately 23.30 to 03.00. Although there is some variation in the results, this trend is significant. The McCollough effect does therefore, show a time of day effect. It is interesting to note the upper and lower limits of the OCCA strength during the period in which they were recorded. These experiments were performed after a standard sleep the night before, which was 8hrs. for subject NJL and 7.5hrs. for subject MJM. The average value of the upper limit of the results, from between 20.00 and 20.30 correspond to the average value obtained in the morning after these sleep durations for each subject (see Figs. 5.2a and 5.2b). The lower level on each graph corresponds closely to the 'base level' observed after short sleep durations. Possible implications of these results will be discussed later (Section 6.7).

Fig. 6.2. Sleep duration fixed: induction hour (following evening) variable





6.3.2. Induction in the evening, shift in sleep period

These experiments were performed under identical conditions to section 6.3.1 but the standard sleep period was 'shifted' and was between 02.00 and 10.00. Subjects had had this shifted sleep cycle for at least 10 days before the first run.

The results for 2 subjects (Fig. 6.3) show the same trend in the initial OCCA strength as Fig. 6.2 but the reduction occurs later, from between 01.00 and 04.00. One subject (MJM) had shifted his sleep cycle after the previous experiment. The reduction in the McCollough effect is shifted by approximately the same number of hours as his sleep cycle. This suggests that the reduction in the OCCA strength at night is a result of some change in an internal mechanism which is related to the sleep cycle.

6.3.3. Decay rates of the OCCA

It has been reported that the decay rate of the McCollough effect decreases when the induction period occurs late in the day (MacKay, 1978). Since the results of Section 6.3.1 indicated that the initial strength of the McCollough effect varies when it is induced from 23.30 and 03.00 it was decided to record the decay rates over this period. The experimental conditions were identical to those of section 6.3.1.

The results for two subjects (Fig. 6.4) show that the decay rate and initial strength varies systematically when induced in the late evening - early morning. The decay rates decrease when the induction period occurs at a late hour. The decay rate starting at

Fig. 6.3. Induction hour variable: 2hr. shift in sleep cycle

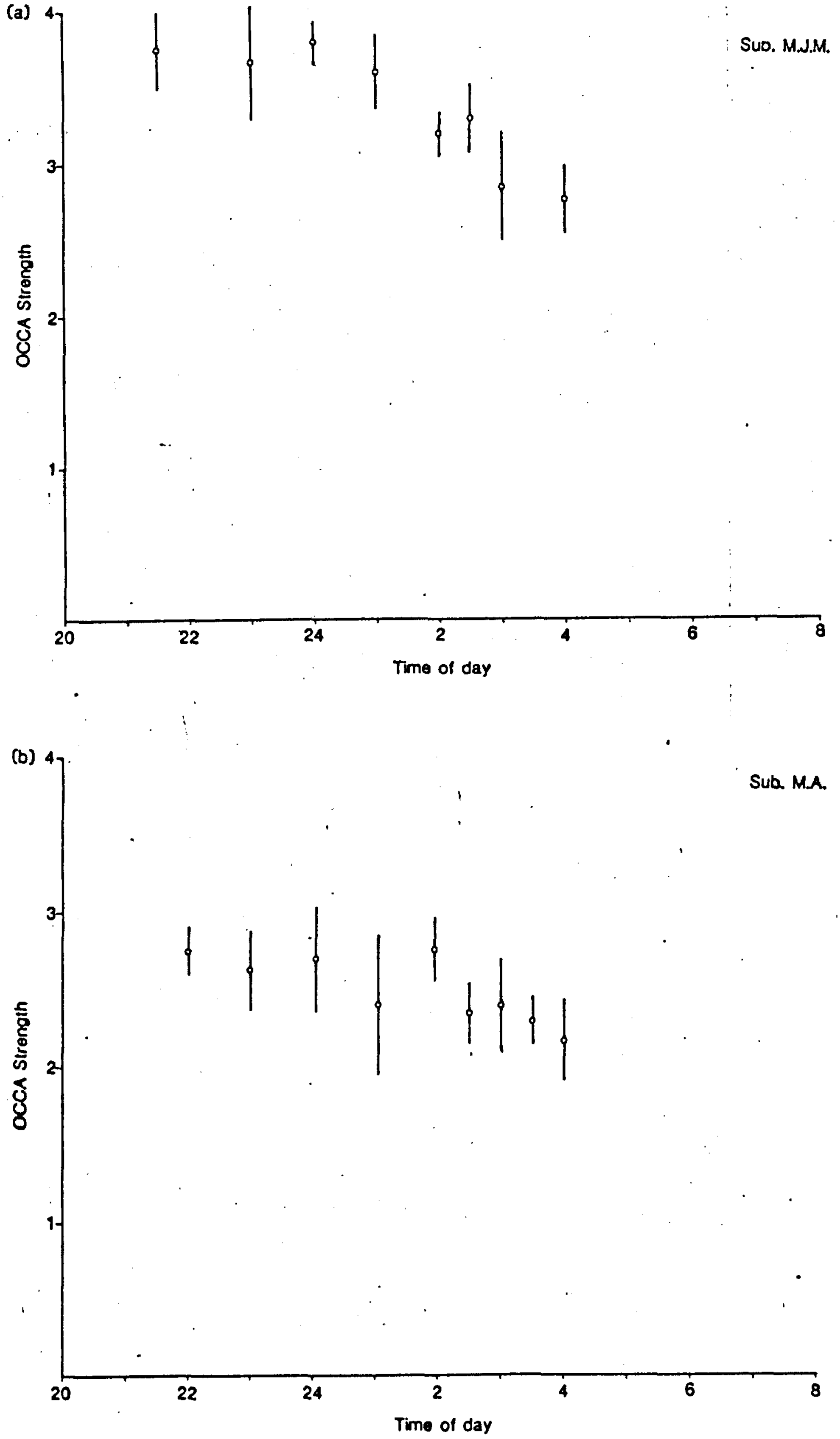
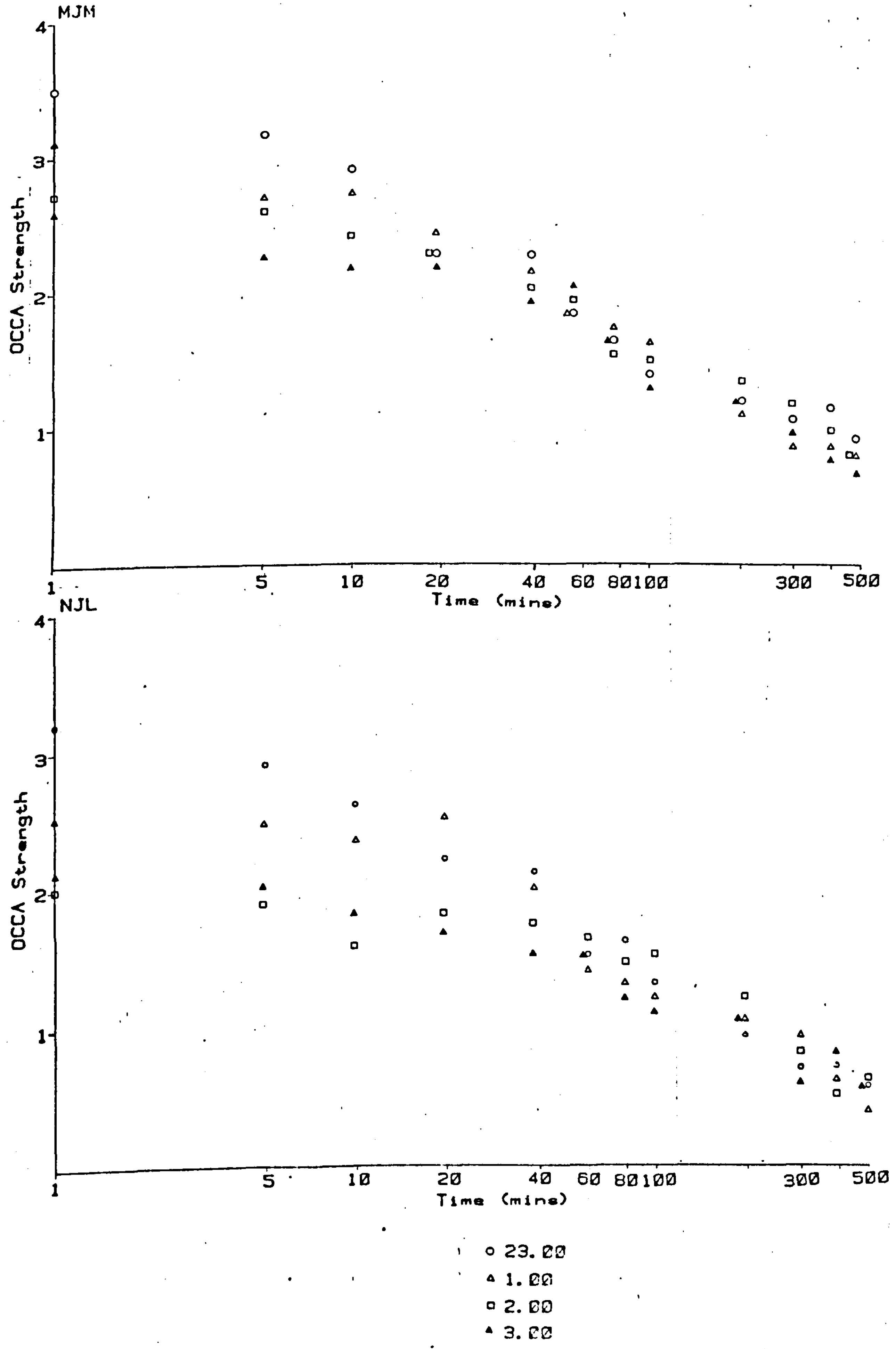


Fig. 6.4. Variation of decay in the evening



23.30 does not vary from the decay rate after 8hrs. sleep starting at 09.00. (see Fig. 5.5).

6.4. Effects of eye patching in the evening

It was possible that the reduction in the OCCA strength at night was due to an increase in the visual stimulation entering the eye. To test this possibility one eye was totally occluded with a light-tight patch for variable periods before induction. The induction period was varied from between 23.30 to 04.00 and the eye was occluded from 20.00. Since the waking hour the previous morning was set, the eye received the same period of visual stimulation before each run. It was not possible to control the type of stimulation received before patching. Patches were removed, in the laboratory in standard illumination, 15 mins. before the induction period to allow the occluded eye to recover from dark adaptation.

The results (Fig. 6.5) show that occluding an eye in the evening has no effect upon the initial McCollough effect strength since they show the same trend and are approximately the same values as those shown in Fig. 6.2a. They indicate that the reduction of the induced OCCA strength at night is not caused by an increase in light stimulation and suggest that it is caused by an internal mechanism.

6.5. Induction late evening after variable sleep the night before

The experiments reported so far in this chapter have been after a standard sleep the night before and have shown a time of day effect. Experiments reported in Chapter 5 have shown that the

Fig. 6.5. Effect of keeping eye in darkness early evening

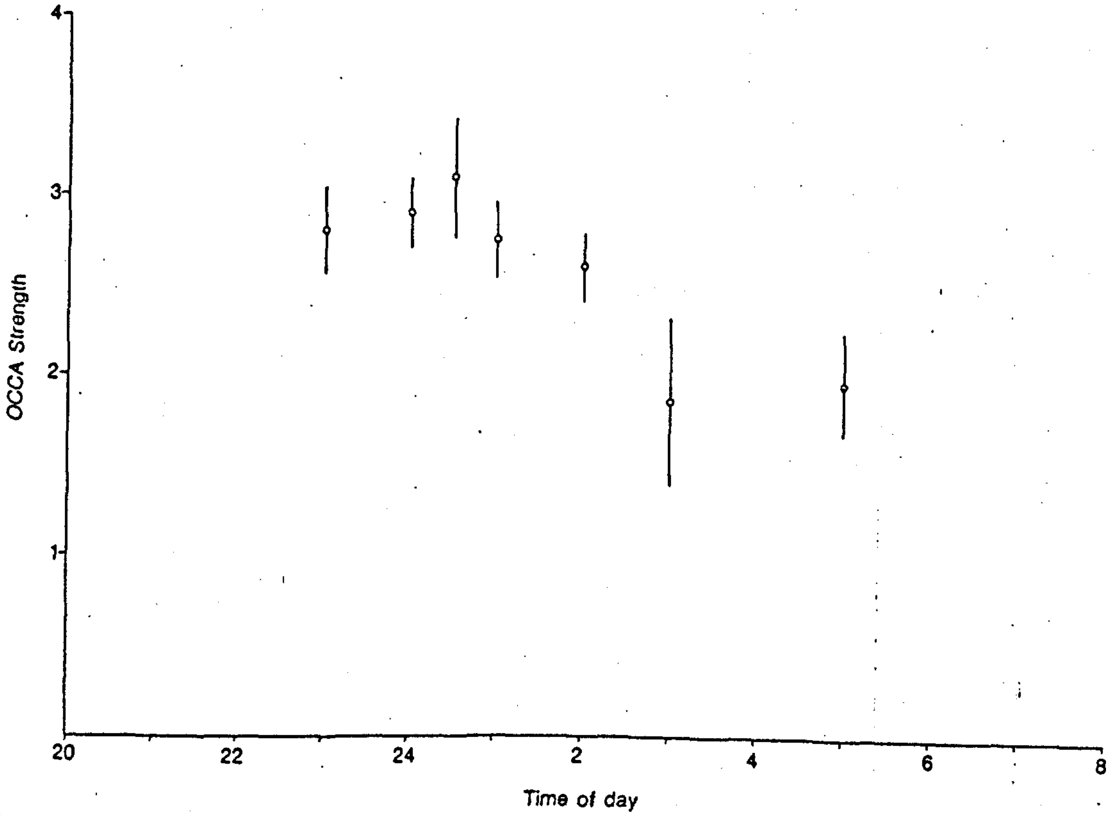
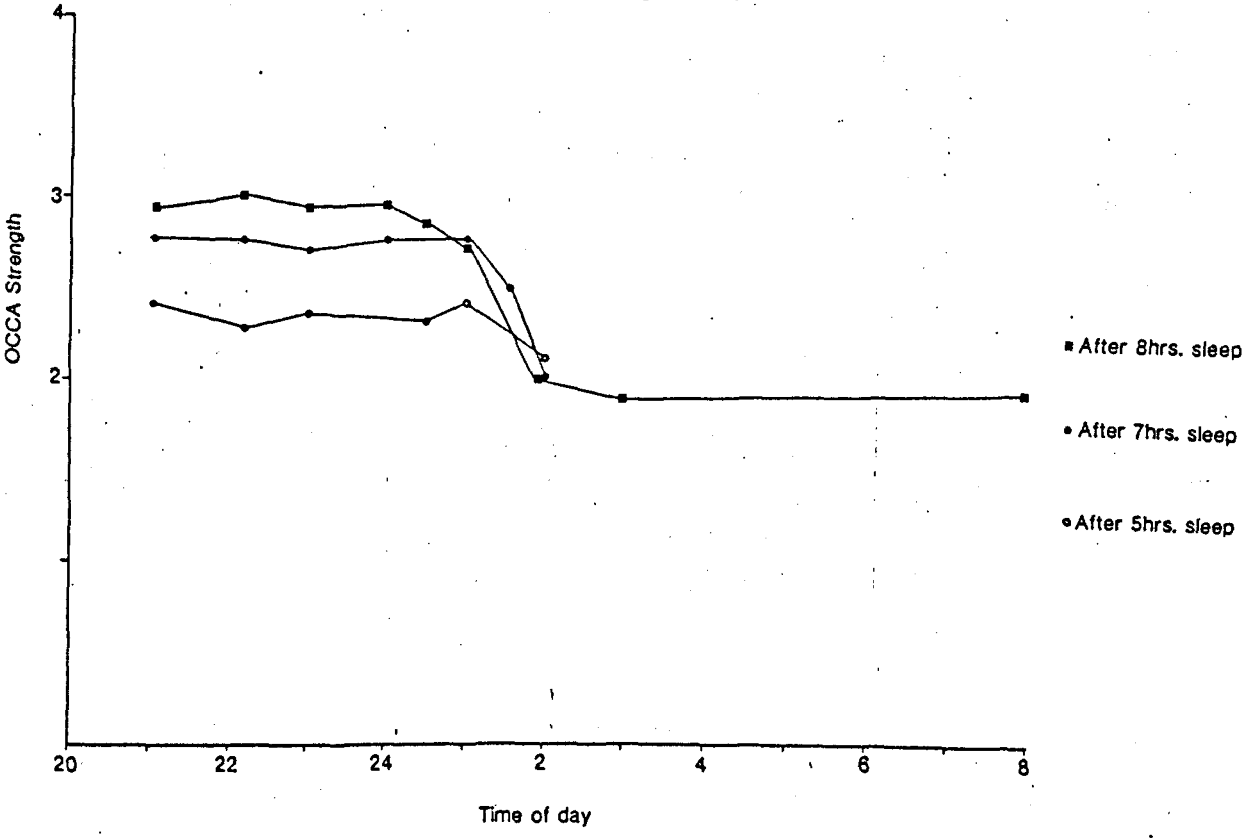


Fig. 6.6. Sleep duration variable: induction hour (following evening) variable



strength of McCollough effects induced in the morning were strongly influenced by the sleep duration the night before. It was decided to investigate any interaction betwee these factors and to determine whether the sleep effect also influenced the OCCA, when it is induced in the evening.

The experimental conditions of section 6.3.1 were repeated, but the sleep duration before each run was varied. Variation in the sleep duration was achieved by varying the bedtime and fixing the waking hour at 08.00.

The results (Fig. 6.6) show the effect of varying the induction hour from between 20.00 and 08.00 after 8,7 and 5 hrs sleep. The average high level of all 3 curves (from between 20.00 and 23.00) correlate with the sleep duration of the previous night. These average levels were slightly higher than the average initial strength found in the morning after these sleep durations for this subject (see Fig. 5.2a). However, this variation was not significantly different and the sleep duration does influence the OCCA when induced in the evening. The results also show some interaction between the 'sleep effect' and the 'time of day' effect. The initial aftereffect strength when induced after short sleep durations, is lower and is not reduced until later in the evening (01.30 after 7hrs. sleep and 02.00 after 5hrs. sleep). It appears to decline after intercepting the 8hrs. sleep curve. The 'sleep effect' and the 'time of day effect' seemed to be linked in some way, which may indicate a common underlying cause.

6.6. Decay at 12pm. after different sleep durations

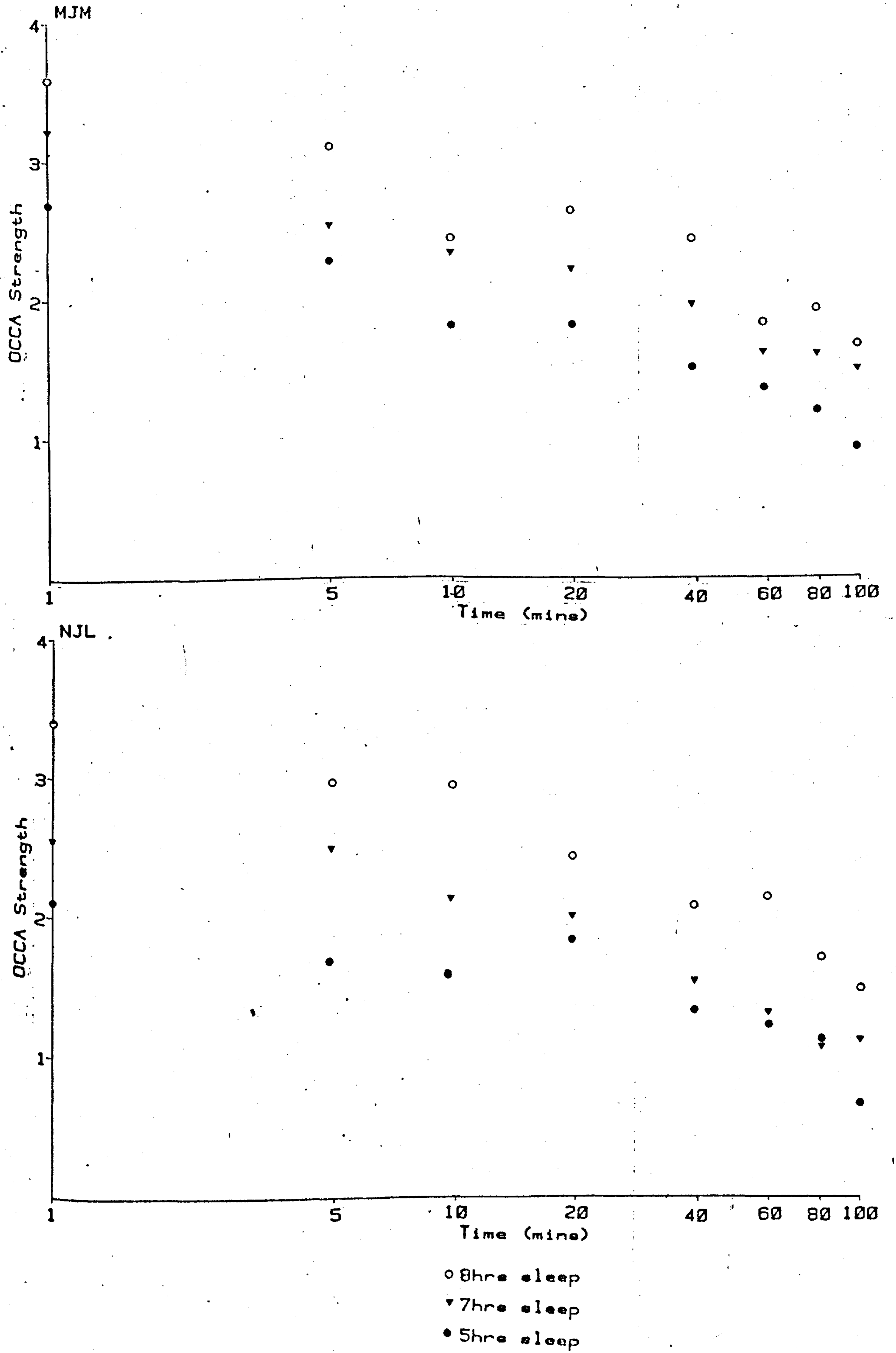
If, as the results of Section 6.4 suggest, the sleep effect and the time of day effect have a common basis, then the results of section 6.3.3 and section 5.2.5 appear to be inconsistent. The results of section 5.2.5 showed that sleep duration had no effect on the decay rate of the McCollough effect. However, the results of section 6.3.3 showed that the decay rate does change during the evening. This inconsistency was investigated by examining the decay rates of the OCCA at the same time at night (00.00 hrs) after various sleep durations.

The results (Fig. 6.7) show that the decay rates of the McCollough effect after 8,7 and 5hrs. sleep do not vary when induced at midnight. These results are consistent with the results of section 5.2.5 and show that prior sleep duration does not influence the decay rate, but does affect the initial OCCA strength. The time of day affects both the decay rate and the initial strength.

6.7. Conclusion and Discussion

The experiments of this chapter have shown that the strength of the McCollough effect shows a time of day effect and undergoes a circadian reduction late in the evening. The timing of the reduction depends upon the sleep cycle. Reduction in the initial strength was not caused by increased visual stimulation. This time of day effect is linked with the effect of sleep duration on the strength of the aftereffect, as McCollough effects induced in the evening after a reduction in sleep do not show a diurnal drop in strength until later. There is evidence that the decay rate of the

Fig. 6.7. Comparison of decay started at 12pm after 8, 7, and 5hrs sleep



McCollough effect also shows a time of day effect. Thus, although both sleep duration and the time of day affect the plasticity of the mechanism responsible for the OCCA, only the time of day affects the long term retention. The upper and lower limit of OCCA strengths for each subject in the time of day experiments and the sleep duration experiments, were not significantly different. This may offer further evidence of a link between the two factors.

There is little evidence of any other visual task undergoing a circadian change although other psychological and physiological factors are known to vary (Blake, 1967; Colquhoun, 1971). Various aspects of memory are known to change throughout the day. A number of reports suggest that immediate recall is better in the morning than the afternoon (Folkard, Monk, Baddeley and Rosenthall, 1977; Hockey, Davis and Gray, 1971; Bradbury, Hatter, Scott and Snashall, 1970). It has also been reported that long-term retention is poor when measured at 04.00 as compared with 20.30 (Monk and Folkard, 1978). The similarity of these reports with the results of this chapter may reflect the associative nature of the McCollough effect.

It is clear that the time of day affects both the decay and the initial strength of the McCollough effect. This could result in some inter and intrasubject variability if experiments were performed at different hours of the day.

CHAPTER 7. ABNORMAL VISION AND THE MCCOLLOUGH EFFECT

7.1. Introduction

The brief summary of exploratory experiments reported in Chapter 4 revealed a large degree of intersubject variability of the McCollough effect. This variation may have been due to differences in the visual perception of the subjects, or visual abnormalities which may be either optical or neural in origin.

During one series of experiments it was noted that two subjects consistently showed differences in OCCA strength in each eye after binocular induction. Later, it was found that these subjects were amblyopic. Subjects were, as reported in Chapter 3, screened for abnormal colour vision and acuity but the tests used (Ishihara plates and Snellen charts) are relatively crude and cannot detect some visual abnormalities. Stereoblind subjects, for example, may have normal or corrected acuity in both eyes, and their condition is apparent only when they are tested with specifically designed apparatus or figures (for example, stereograms). Amblyopia, which is characterised by a developmental loss of acuity in one eye, also shows a lack, or severe reduction, of binocular functions (Duke-Elder, 1973). There is a growing body of evidence showing that both amblyopic and stereoblind observers manifest peculiarities of interocular transfer of a number of achromatic aftereffects (for example, Ware and Mitchell, 1974). Amblyopic subjects also perceive certain stimuli abnormally (Levi, Harwell, Pass and Venverloh, 1981; Bradley and Freeman, 1981).

The McCollough effect has been shown to exhibit specific monocular and binocular properties (see Chapter 2 and Coltheart, 1973 for review). A number of reports have revealed some intersubject variability when dichoptic stimuli were used (MacKay and MacKay, 1975b) and there has been contradictory evidence about dichoptic OCCA's (Over, Long and Lovegrove, 1973) and interocular transfer (Mikaelian, 1975). As stereoblind and amblyopic subjects show different interocular transfer of some aftereffects from normal observers, the effects of these visual abnormalities on the McCollough effect were investigated to determine whether they could be responsible for some intersubject variability. A variety of normal, amblyopic and stereoblind subjects were investigated using binocular, monocular and dichoptic stimulation.

7.2. Subject Data

	Uncorrected Acuity		Corrected Acuity		Stereopsis
	Left	Right	Left	Right	
Normal					
NJL	6/4	6/4	-	-	Good
MJM	6/5	6/4	-	-	Good
PDF	6/5	6/5	-	-	Good
SG	6/4	6/4	-	-	Good
Stereoblind					
TB	6/9	6/6	-	-	Poor
MH	6/12	6/9	6/5	6/6	None
PS	6/12	6/60	6/5	6/4.5	None

IM	6/36	6/18	6/6	6/5	Poor
Amblyopic					
DRB	6/9	6/60	6/5	6/60	None
BK	6/5	6/60	6/5	6/60	Poor
GJS	6/18	6/6	6/18	6/5	Poor
LBS	6/36	6/5	6/36	6/4	None
ATS	6/4	6/12	-	-	Poor
CJH	6/6	6/60	6/5	6/60	None
MS	6/36	6/9	6/36	6/6	None
KIG	6/60	6/18	6/60	6/9	None

7.3. Binocular stimulation

Normal subjects usually develop similar McCollough effect strengths in each eye after binocular induction, but some preliminary experiments indicated that amblyopic subjects developed substantially different aftereffect strengths in the normal and amblyopic eyes. In order to study this phenomenon systematically, monocular strengths were recorded after binocular stimulation using a variety of subjects. Amblyopic subjects were instructed to wear their corrective lenses throughout the experiment. A standard 15min. induction period, consisting of 1s 'on' and 4s 'off' intervals, was used.

7.3.1. Initial Strength

The initial strengths for each were recorded monocularly using 4 normal subjects, 4 stereoblind subjects and 8 amblyopic subjects.

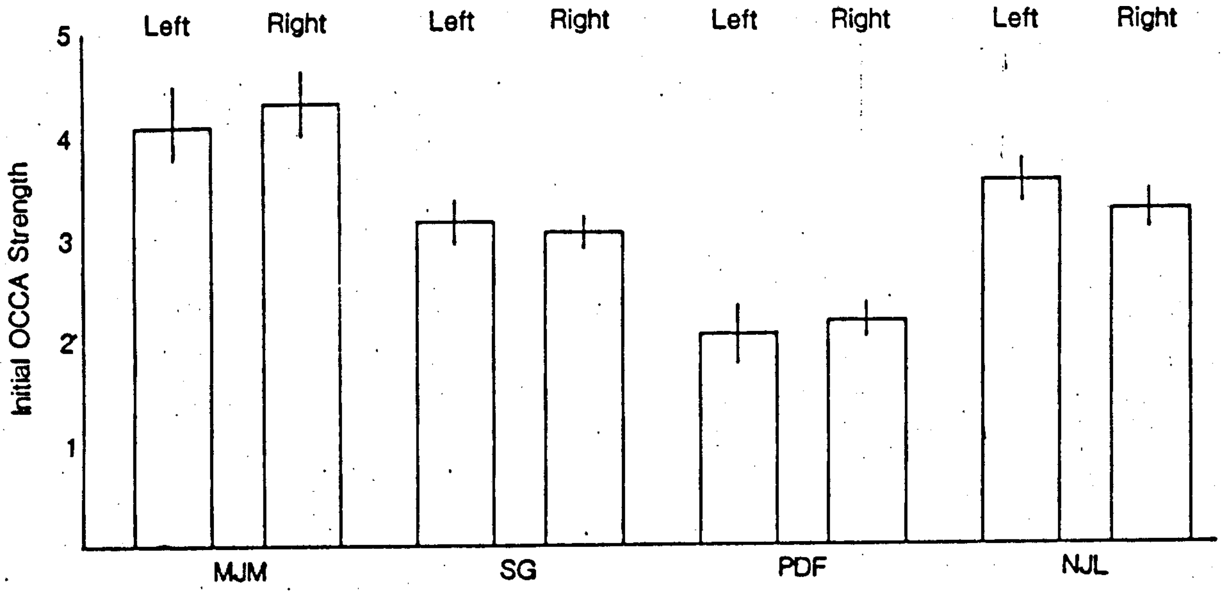
Each subject repeated the run at least once and the data (shown in Fig. 7.1) were averaged. The results show that the 4 normal subjects (Fig. 7.1a) all developed similar McCollough effects in each eye. The small differences which were observed varied in strength and polarity from run to run. Every amblyopic subject, however, consistently developed a significantly higher aftereffect strength in the normal eye than in the amblyopic eye (shown cross hatched). A similar result has been reported by Campbell, Hess and Shute (1978) who found that after binocular stimulation, amblyopic subjects developed smaller OCCA's in the amblyopic eye. They also reported that after testing the normal eye, the effect in the amblyopic eye was greater than the normal, which presumably was due to some form of transfer (see below). Two of the stereoblind subjects, like the normal subjects, developed a similar aftereffect strength in each eye, but the other 2 subjects developed different strengths in each eye. The difference was not as great as that observed for the amblyopic subjects.

7.3.2. Amblyopia and Interocular Generalization

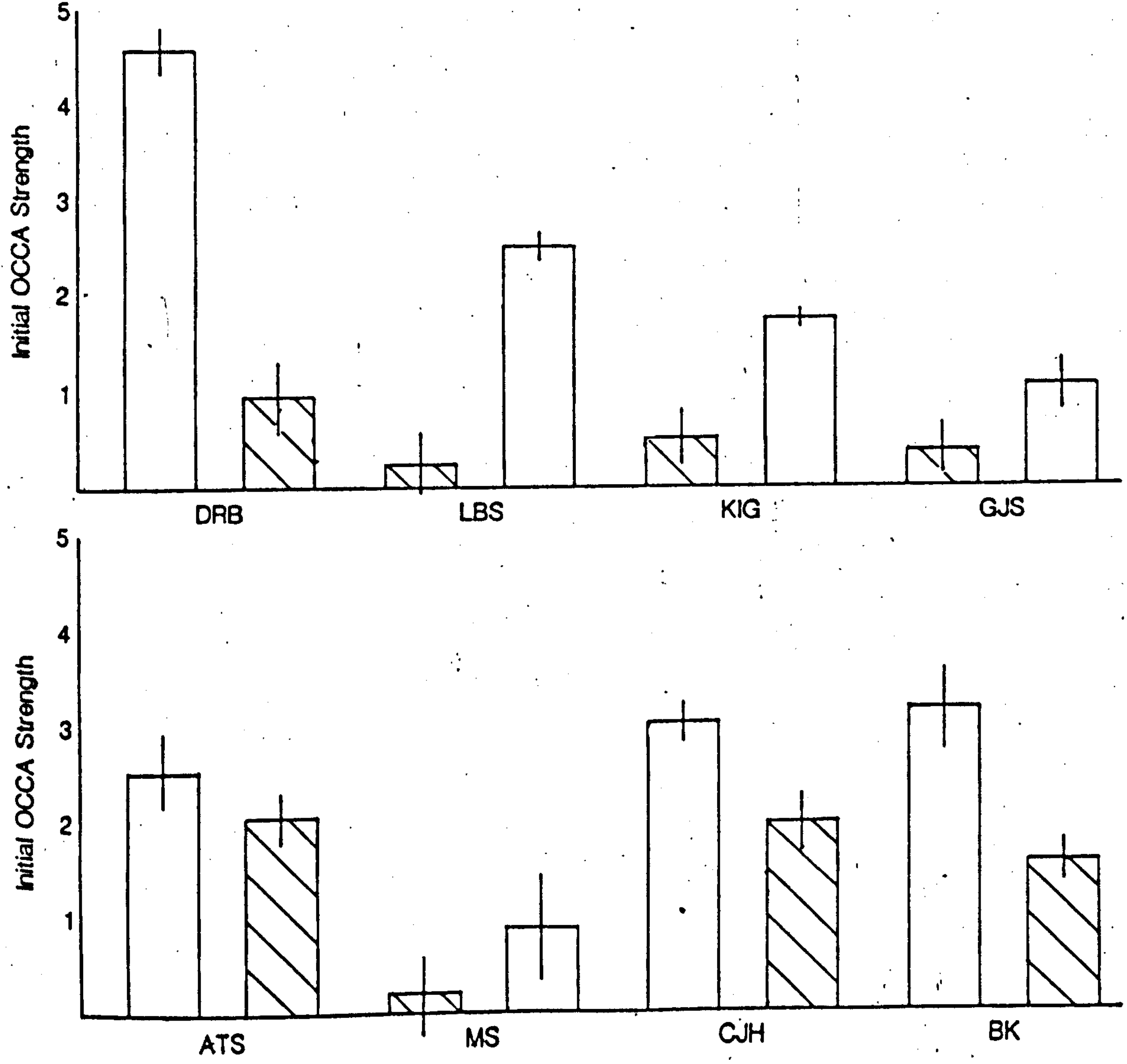
For some time it has been generally agreed that the McCollough effect does not transfer interocularly to any great extent. One of the few exceptions to this observation has been reported by Mikaelian (1975), who claimed that aftereffects were present in the unstimulated eye if subjects had previously viewed a test pattern binocularly. Mikaelian termed this phenomenon 'interocular generalization'. MacKay (1978) repeated these experiments and found no evidence of such an effect in normal subjects. Recently, however, another report has suggested that amblyopic subjects show a

Fig. 7.1. Monocular test after binocular induction

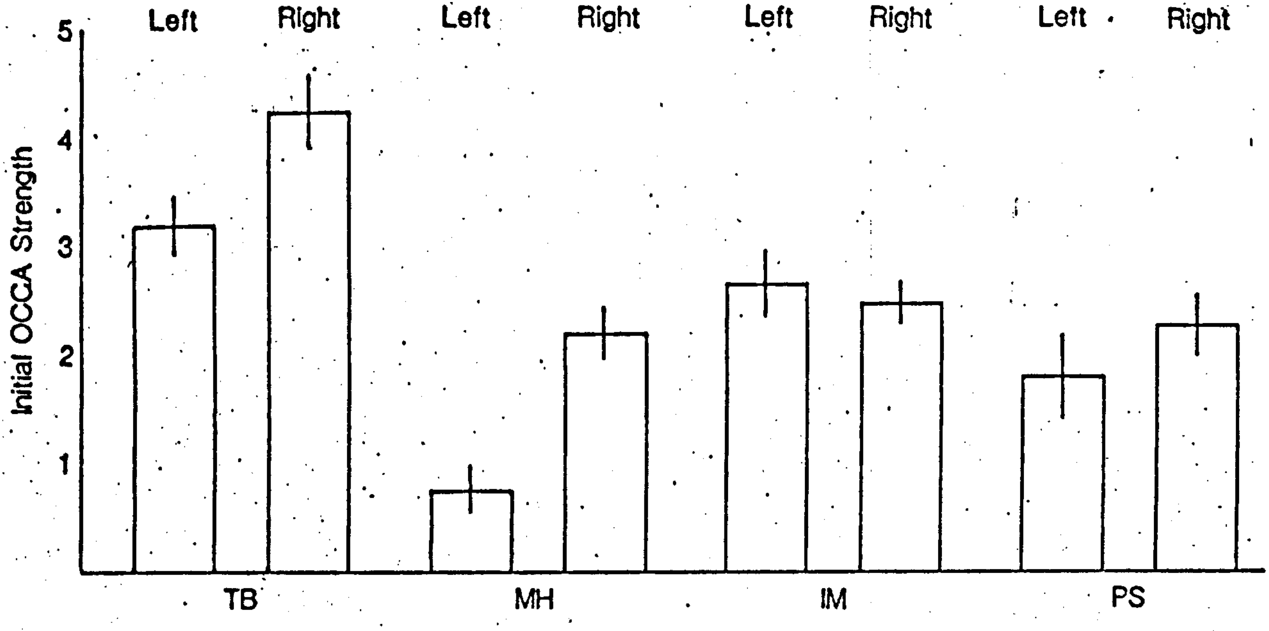
(a) Normal subjects



(b) Amblyopic subjects



(c) Stereoblind subjects



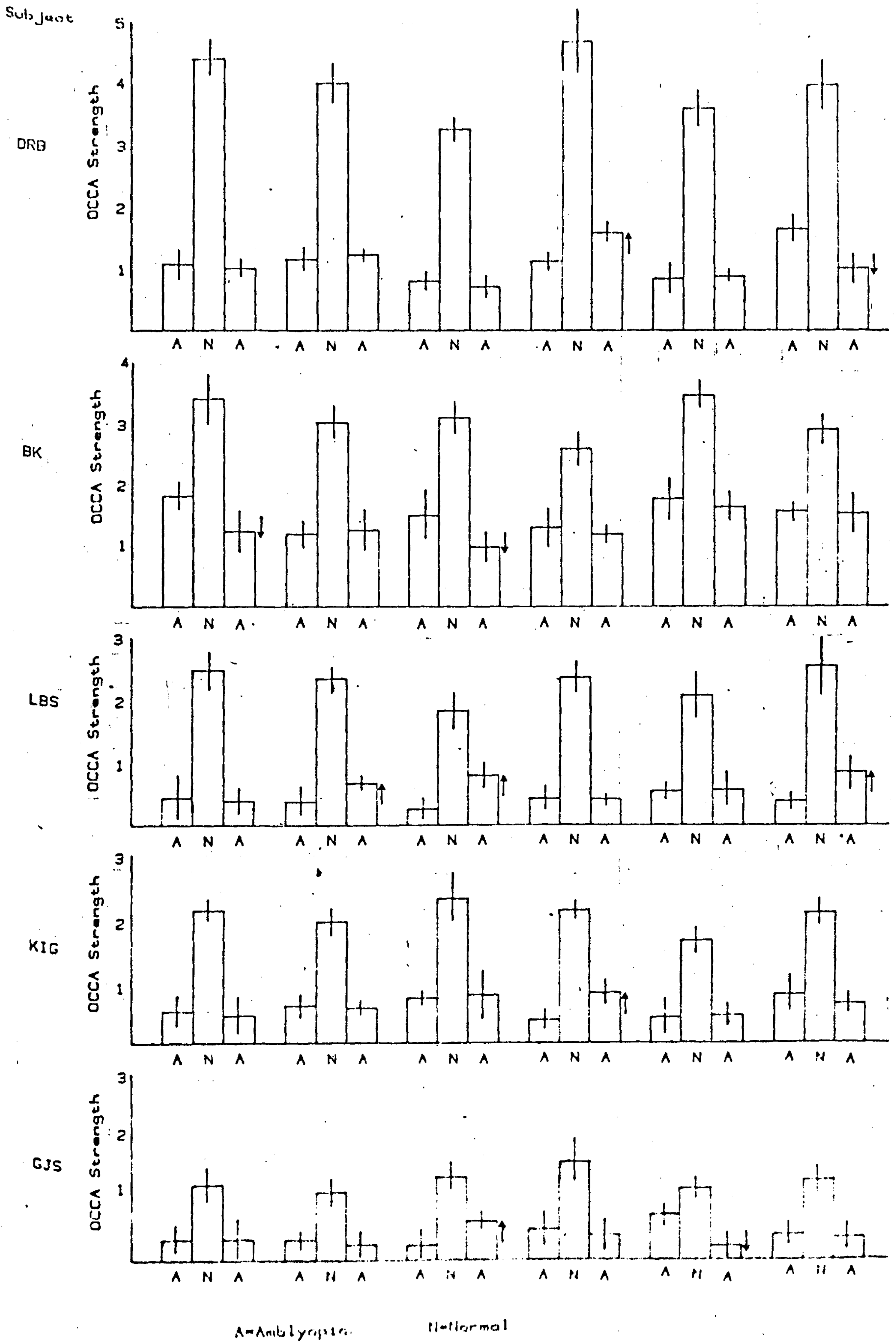
similar form of generalization. Campbell et. al. (1978) found that, following binocular induction, amblyopic subjects developed a small OCCA in the amblyopic eye and a large OCCA in the normal eye; but after test measurements in the normal eye, the aftereffect in the amblyopic eye was even higher than that of the normal.

On reviewing the data of the previous section and after further experiments performed to investigate such effects with amblyopic subjects, the author found no consistent evidence of an increase for the amblyopic eye after a test of the normal eye. Analysis of 30 binocular runs (Fig. 7.2) showed an increase for the amblyopic eye on only 6 occasions (marked with an up arrow) and this increase was never sufficiently large to 'boost' the OCCA to a higher level than that in the normal eye. In most runs the aftereffect remained similar in strength and in 4 runs (marked with a down arrow) the OCCA actually decreased in strength.

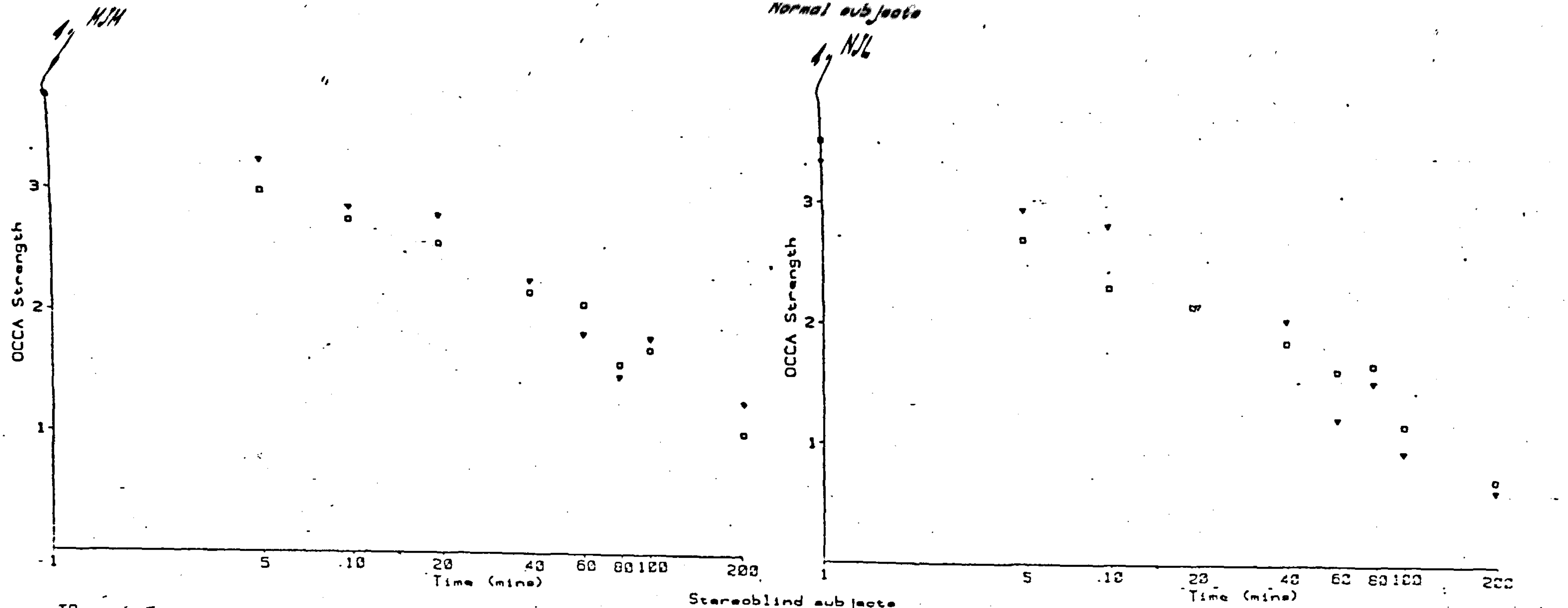
7.3.3. Decay

Monocular decay rates of each eye were measured using 2 normal, 2 stereoblind and 4 amblyopic subjects (Fig. 7.3). The results show that normal subjects, as noted in Chapter 4, have a similar decay rate in each eye. Although the amblyopic subjects developed smaller aftereffects in the amblyopic eye, the decay slopes for each eye were similar. Both the stereoblind subjects who had similar, and those who had different, aftereffect strengths in each eye had decay slopes which did not vary.

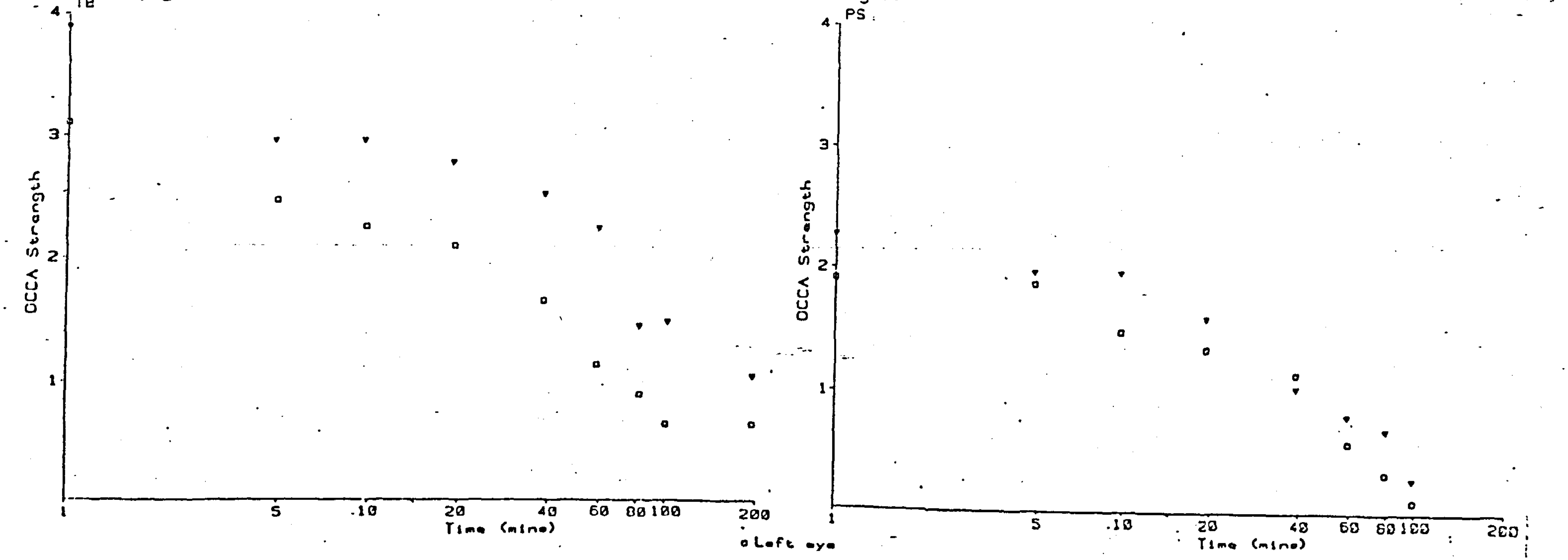
Fig. 7.2. The effect of testing order upon the OCCA strength



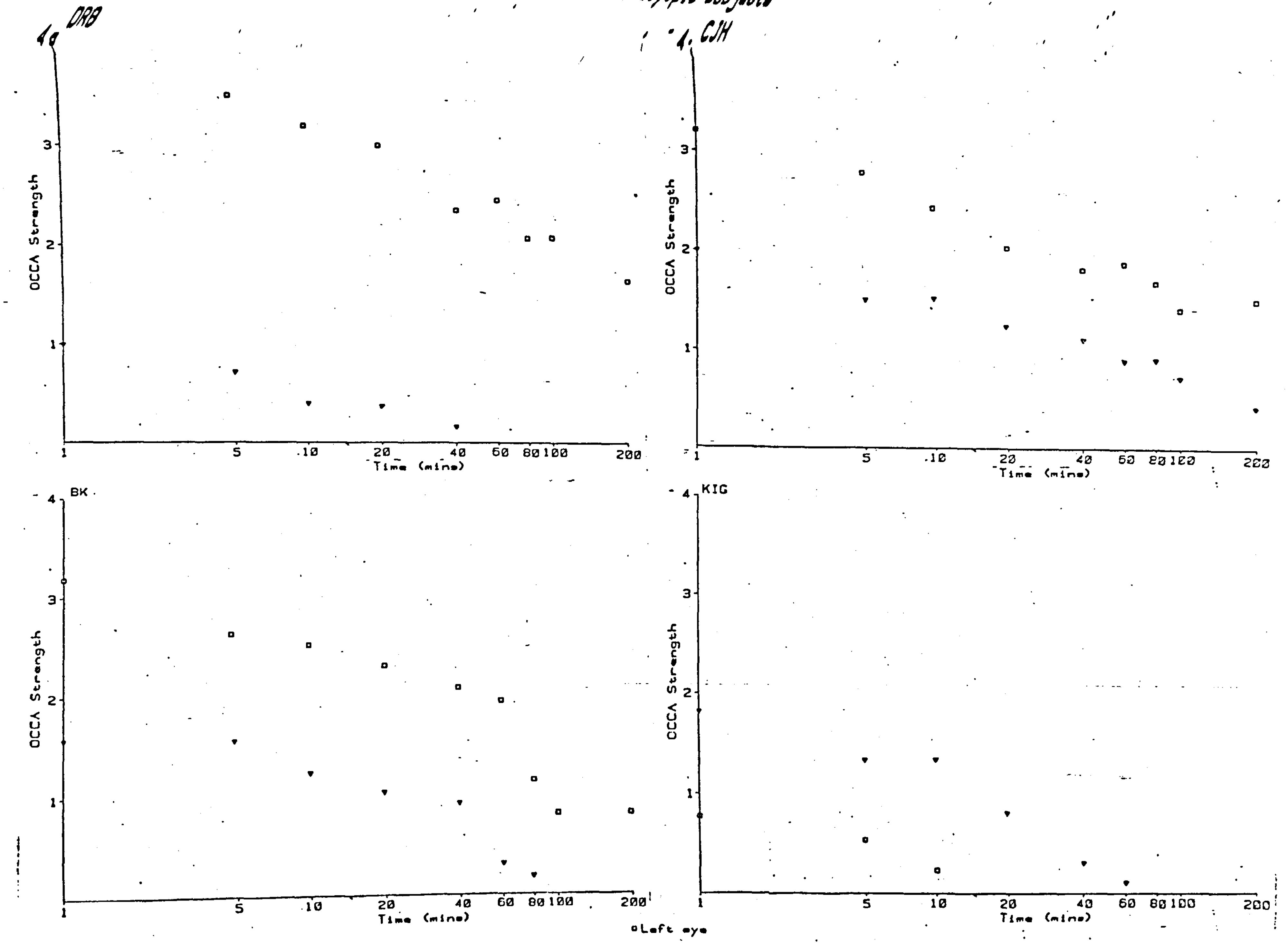
Normal subjects



Stereoblind subjects



Amblyopia subjects



7.3.4. Conclusions

The experiments show that, although normal subjects develop similar strengths of aftereffect in each eye after binocular stimulation, some stereoblind and all amblyopic subjects develop much larger McCollough effects in the dominant than the non-dominant, or amblyopic, eye. The visual defects affect only the induction of the OCCA since the decay rates for each eye, as in normal subjects, were similar. The small aftereffect in the amblyopic, or non-dominant, eye may have been due to either binocular rivalry or neural deficiencies. Some evidence suggests that suppression of visual input by binocular rivalry does not reduce the strength of the McCollough effect (White and Riggs, (1975). Following electrophysiological evidence, which shows that early visual experience can modify the neurones of the visual cortex (Blakemore and Cooper, 1970; Hirsch and Spinelli, 1970, 1971), it has been suggested that amblyopia and binocular disorders are caused by abnormal neural qualities, resulting from abnormal visual input to one or both eyes during childhood (Mitchell, Freeman, Millidot and Haegerstrom, 1973; Hohmann and Creutzfeldt, 1975). If the small aftereffect seen in the amblyopic eye was due to rivalry, and not to a neural disorder, one would expect a larger aftereffect in that eye when it was exposed to monocular stimulation. The following monocular experiments were performed to resolve this question.

7.4. Monocular stimulation

McCollough effects were induced and tested monocularly in both the left and right eyes, on different occasions, using 4 normal, 3 stereoblind and 6 amblyopic subjects. The unstimulated eye was occluded during induction by a light-tight patch.

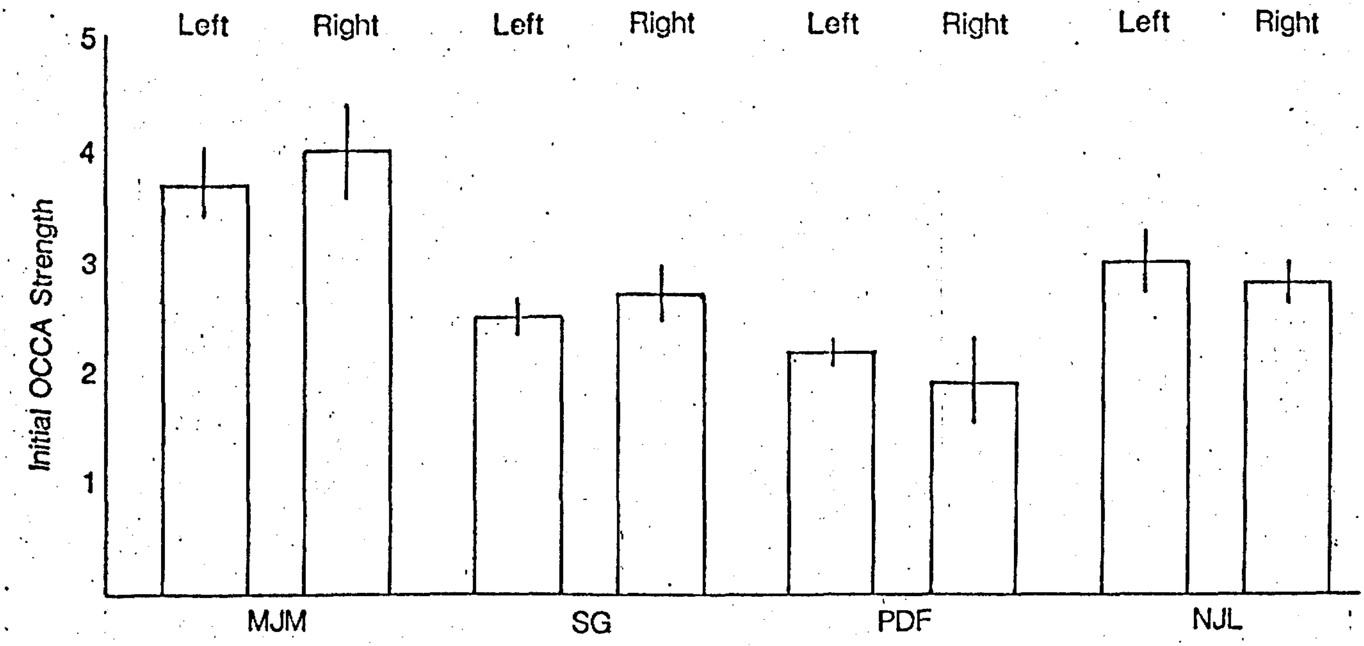
7.1. Initial Strength

The initial strengths yielded by the left and right monocular tests are shown in Fig. 7.4, where results for amblyopic eyes are shown cross-hatched. They show that the normal, and some stereoblind, subjects developed slightly lower monocularly tested initial strengths after monocular rather than binocular induction (cf Fig. 7.1 a and c). Every amblyopic subject, except subject CJH, also gave a slightly lower monocular result in the normal eye. All the amblyopic subjects, however, showed a larger initial strength in the amblyopic eye when the normal eye had been occluded during induction. The same trend was observed in a stereoblind observer (TB) who had displayed consistently different aftereffect strengths in the two eyes after binocular induction.

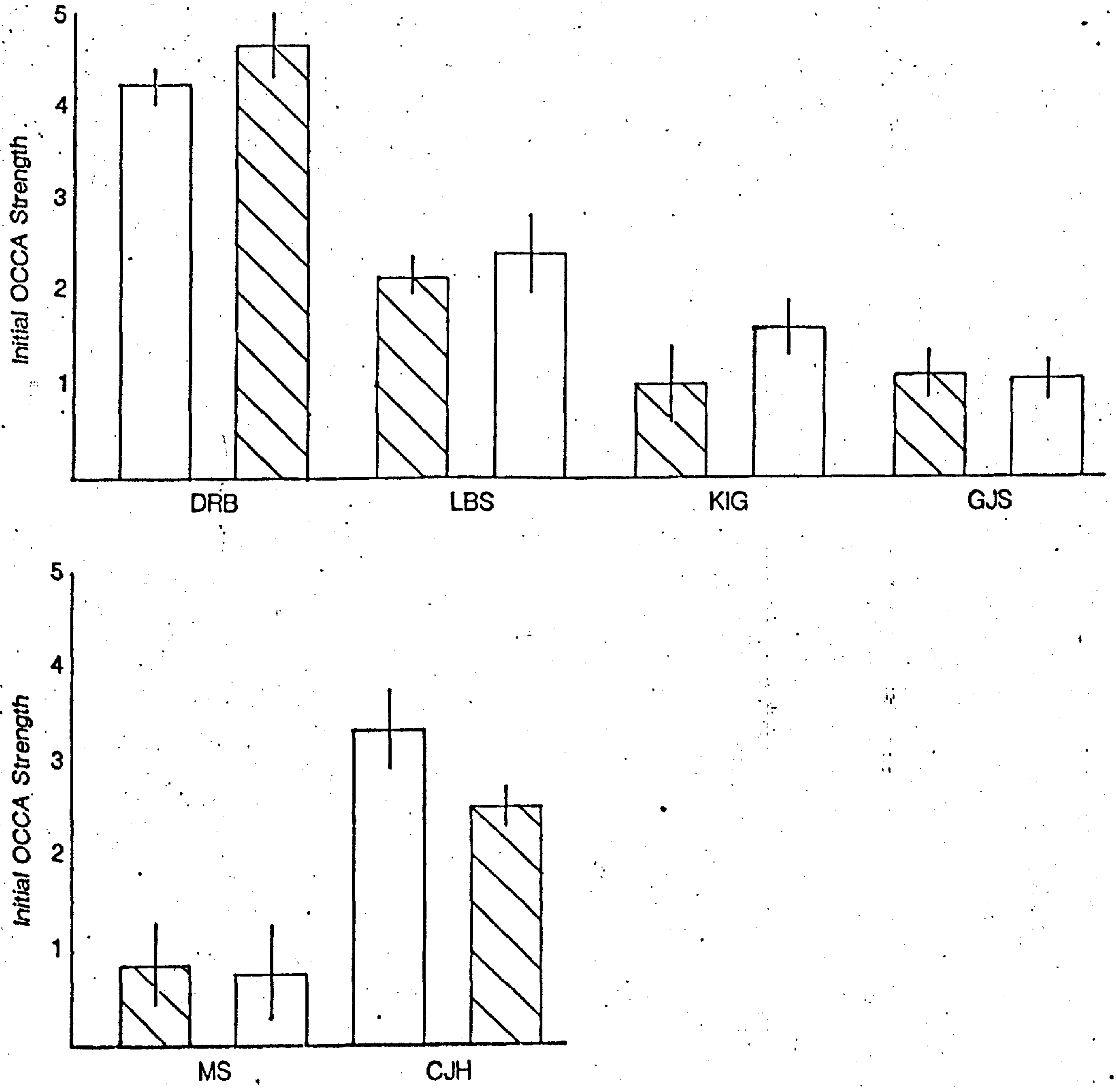
These results suggest that the small OCCA observed in the amblyopic, or non-dominant, eye after binocular induction was due to binocular rivalry and not to neural deficiencies, since any neural deficiences were still present during monocular stimulation. In addition, during monocular induction, any 'pure binocular' neurones are unlikely to be stimulated, so that one could expect the monocular test result to be smaller after monocular than binocular induction. Since normal subjects are not affected by binocular rivalry during binocular stimulation, it is likely that the rivalry observed in amblyopic, and some stereoblind, observers may be related to their abnormal visual perception. It has been shown that

Fig. 7.4. Monocular test after monocular induction

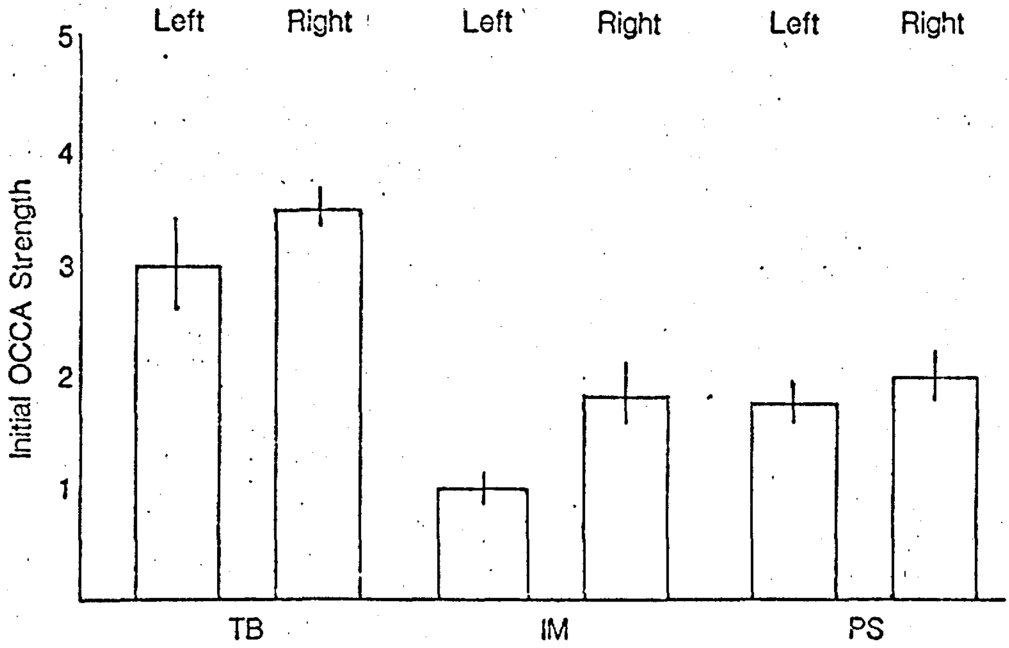
(a) Normal subjects



(b) Amblyopic subjects



(c) Stereoblind subjects



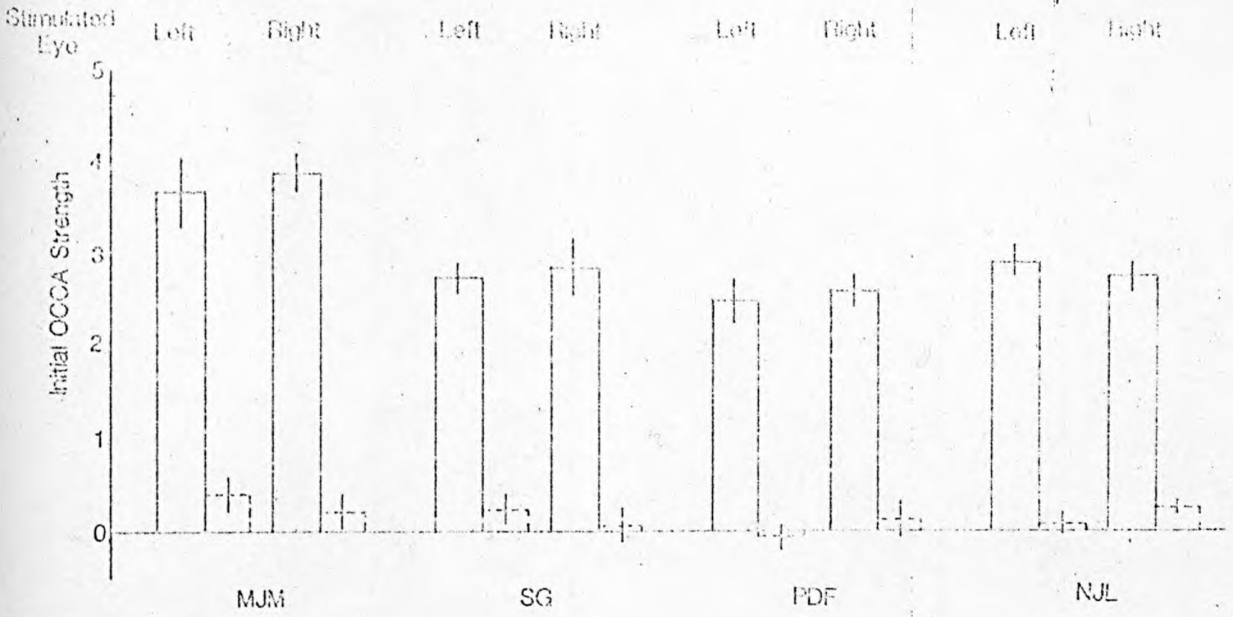
retinal rivalry has no effect on the strength of monocular motion aftereffects (Lehmkuhle and Fox, 1975) and this has been taken as evidence that suppression occurs at a higher level than the cortical neurones thought to cause the MAE.

7.4.2. Interocular transfer

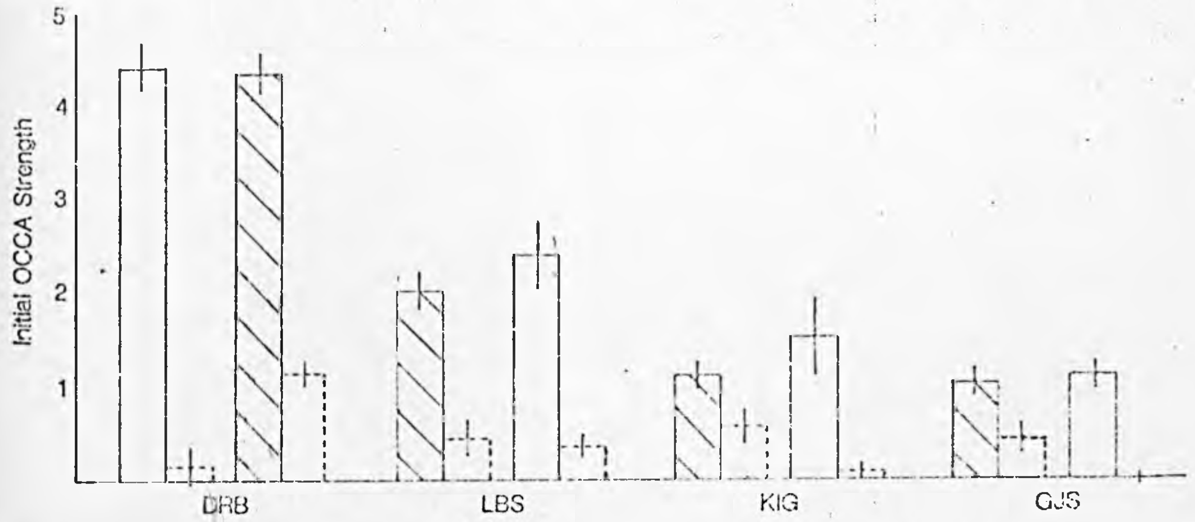
It is generally agreed that the McCollough effect, and other colour contingent aftereffects, fail to show substantial interocular transfer (Murch, 1972), but some reports have shown weak aftereffects (below 10%) in the occluded eye (MacKay, 1978; Favreau, 1978). A number of reports have shown that amblyopia and stereoblindness reduce the interocular transfer of a variety of achromatic aftereffects including: the motion aftereffect (Mitchell, Reardon and Muir, 1975); the tilt aftereffect (Movshon, Chambers and Blakemore, 1972; Mitchell and Ware, 1974); and the grating threshold elevation effect (Ware and Mitchell, 1974). In view of these data, one might expect that amblyopia and stereoblindness should if anything reduce still further the interocular transfer of the McCollough effect, to a barely significant, or zero level. To test this prediction, the experiments in the previous section were repeated but both the stimulated and unstimulated eyes were tested to investigate interocular transfer. Normal, stereoblind and amblyopic subjects were used and the results are shown in Fig. 7.5. The block data represent the stimulated eye and the dotted data the unstimulated eye, or the transferred McCollough effect. Fig. 7.5b. shows the transferred McCollough effect as a percentage of the aftereffect found in the stimulated eye.

Fig 7.5 Transfer after monocular stimulation

(a) Normal subjects



(b) Amblyopic subjects



(c) Stereoblind subjects

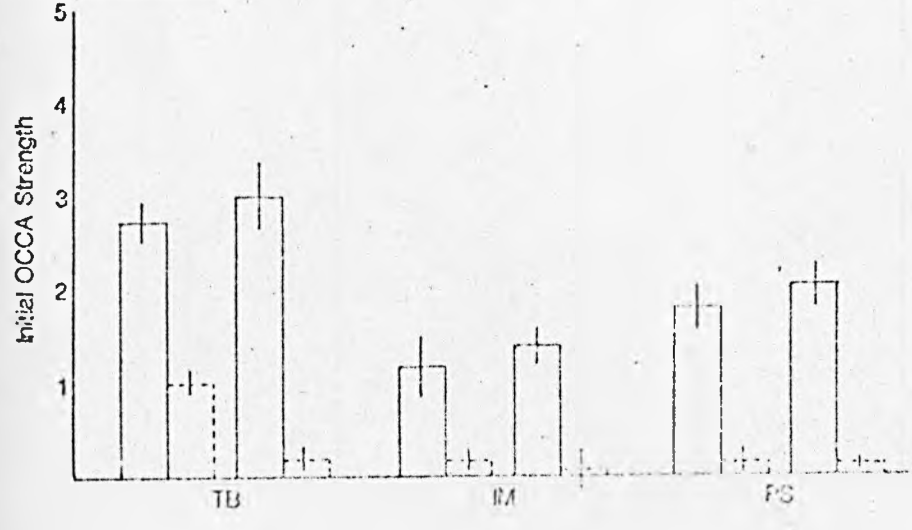
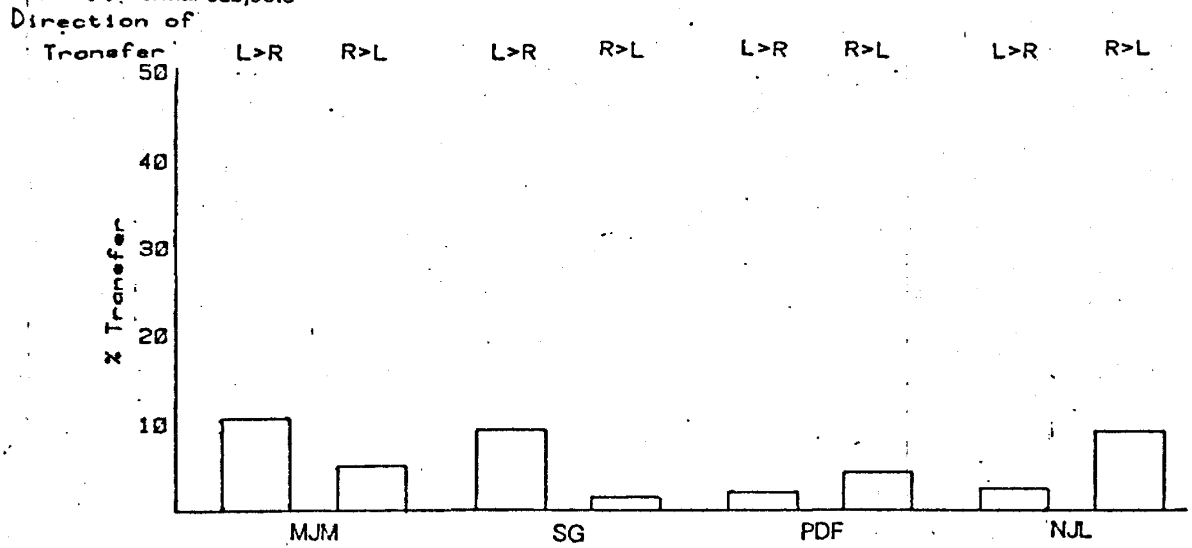
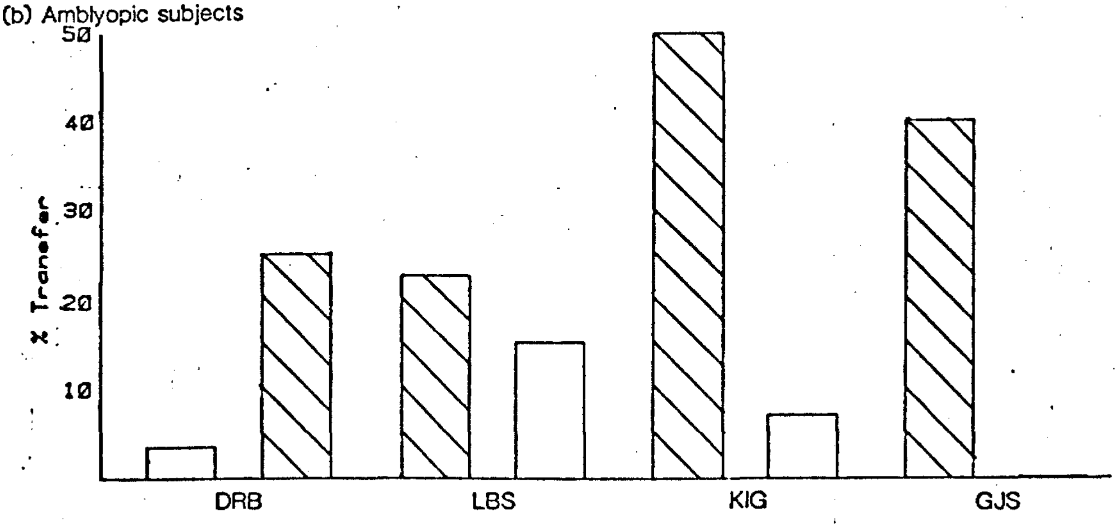


Fig. 7.5b. Percentage of transfer after monocular induction

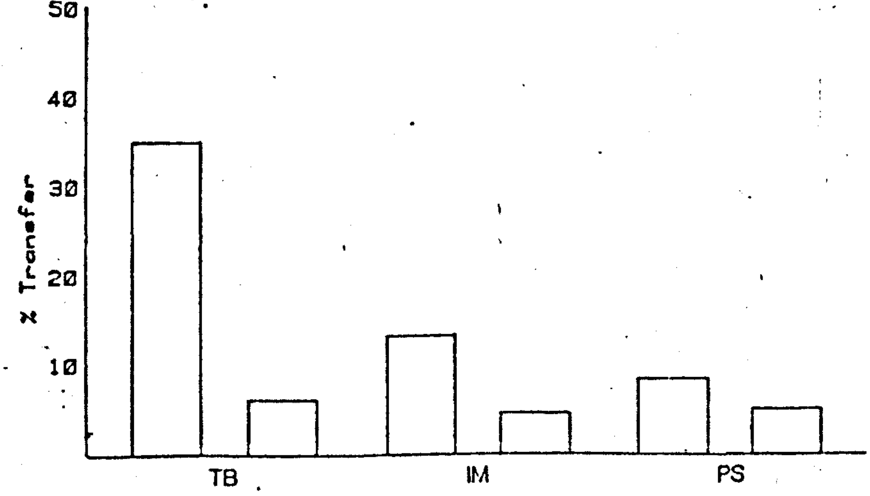
(a) Normal subjects



(b) Amblyopic subjects



(c) Stereoblind subjects



The data obtained for the normal subjects were consistent with past evidence. When either eye was stimulated, most subjects showed small but consistent, aftereffects (below 11%) in the unstimulated eye. One subject showed weak (3-5%) transfer of an aftereffect of opposite polarity. When the normal eye was stimulated, most of the the amblyopic subjects, as predicted, showed weak or no transfer to the amblyopic eye. It was surprising, therefore, to find that all amblyopic subjects showed consistently large transfer (varying from 22 to 50%) from the amblyopic to the normal eye. One amblyopic subject (LBS) did show transfer in both directions but transfer from the amblyopic to the normal eye was larger (22%) than in the opposite direction (15%). The stereoblind subjects again varied, as 2 failed to show substantial transfer from either eye; but subject (TB), like the amblyopic subjects, showed consistent transfer in one direction. Subject TB also showed similarities to the amblyopic subjects as he developed consistently larger monocular OCCA strengths in one eye, after binocular stimulation (see Fig. 7.1). Transfer of approximately 30% was, as in the amblyopic subjects, observed from the eye which developed a smaller aftereffect.

These results show that amblyopic, and some stereoblind, subjects exhibit <u>greater</u> interocular transfer of the McCollough effect than do normal subjects, but <u>only</u> from the amblyopic, or non-dominant, eye. This result was in contrast with past evidence, which indicated that such subjects have reduced transfer of achromatic aftereffects. It is also contrary to the report of Mitchell and Ware (1974), who noted that 'transfer was greater from the dominant eye to the non-dominant eye than vice versa', since these amblyopic and stereoblind subjects showed greater transfer from the non-dominant, or amblyopic, eye to the dominant.

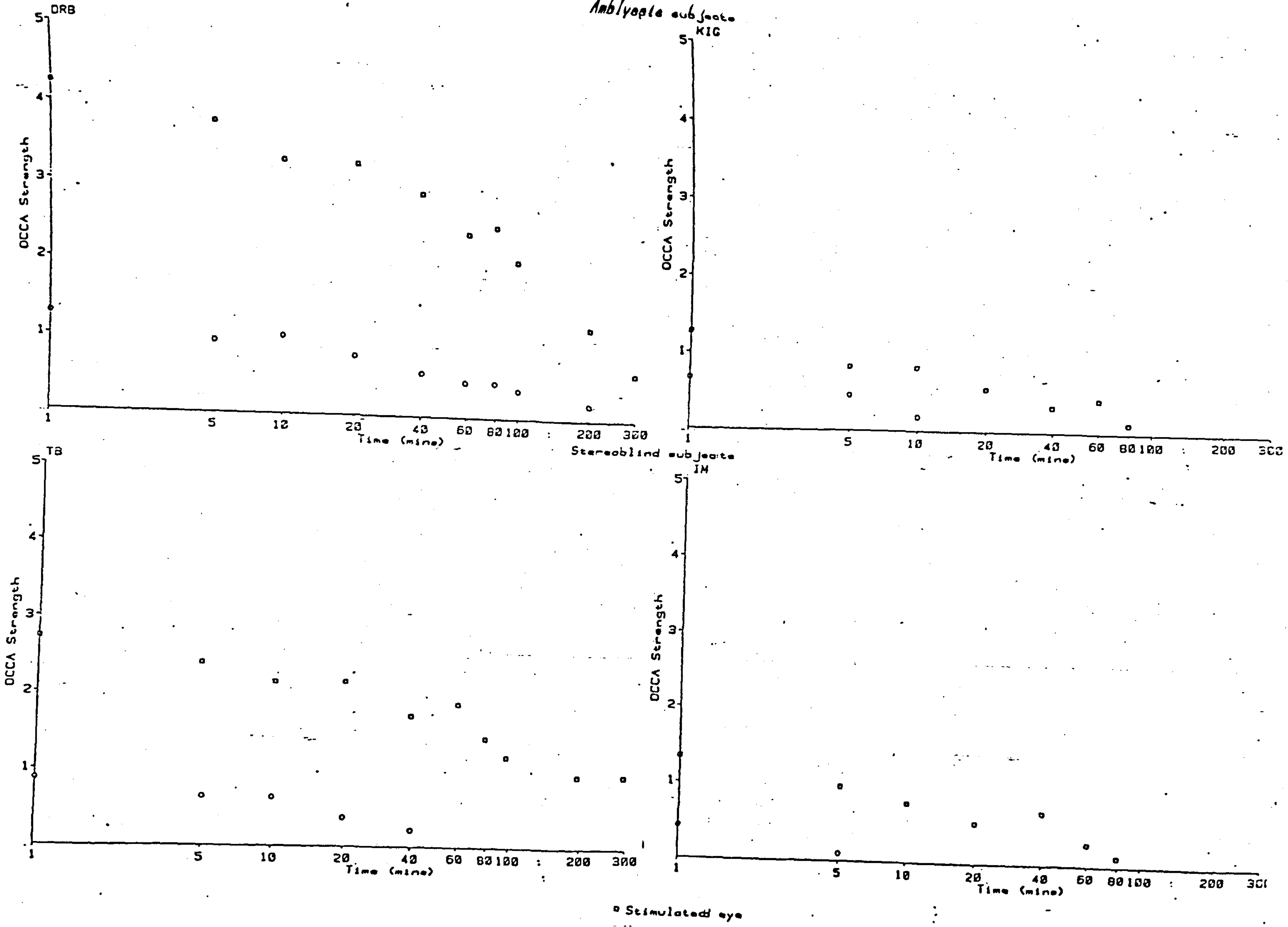
The variability in the results of the stereoblind subjects was probably due to small differences in their binocular capability since Keck and Price (1982) have shown that such subjects had a wide variation in the amount of transfer of a motion aftereffect which was dependant upon their particular disorder. Furthermore, although it is generally agreed that stereoblind individuals do not show transfer of achromatic aftereffects (see above), some recent reports have indicated that some do retain a population of binocular neurones since they show interocular transfer of the grating threshold elevation aftereffect (Anderson, Mitchell and Timney 1980; Hess, 1978).

7.4.3. Decay of transferred McCollough effect

One of the properties of the McCollough effect is that it shows a characteristic time course of decay (MacKay and MacKay, 1973b) which in normal subjects is similar in each eye. For this reason, the large transferred McCollough effect observed in subjects with abnormal vision was investigated to see whether it decayed at the same rate as the effect in the stimulated eye, since it could have been a transitory aftereffect. McCollough effects were induced monocularly in 2 amblyopic and 2 stereoblind observers in the amblyopic or non-dominant eyes respectively. The decay rates of the aftereffect in the stimulated eye and of the transferred McCollough effects in the normal, or dominant, eyes are compared in Fig. 7.6.

The results show that the transferred McCollough effect is not transitory but lasts up to at least 200mins. In all but one subject, however, the decay rate of the transferred McCollough effect was slightly faster than the decay rate in the stimulated

Fig. 7.6. Decay of transferred McCollough effects



eye.

7.5. Binocular Rivalry

It has been demonstrated that binocular rivalry produced by achromatic stimuli does not affect the strength of the McCollough effect (White and Riggs, 1975), though MacKay (1978) reports contrary findings. Rivalry produced by patternless colour has been shown not to reduce the McCollough effect in the stimulated eye and to enhance interocular transfer (White et al, 1978). The monocular experiments reported above indicated that the small aftereffect obtained in amblyopic, or non-dominant, eyes during binocular stimulation was due to some binocular rivalry produced by some, or all, of the inducing stimuli presented to the normal or dominant eye. In order to investigate which aspect of the McCollough effect stimuli, if any, was responsible, a number of experiments, in which one parameter of the inducing stimuli was deliberately manipulated to cause greater rivalry than the other, were performed with amblyopic subjects. The stimuli were presented binocularly, but either the colours were different in each eye and the gratings were of the same orientation, or the gratings were orthogonal in each eye and the colours were the same (see Fig. 7.7).

Fig. 7.7.

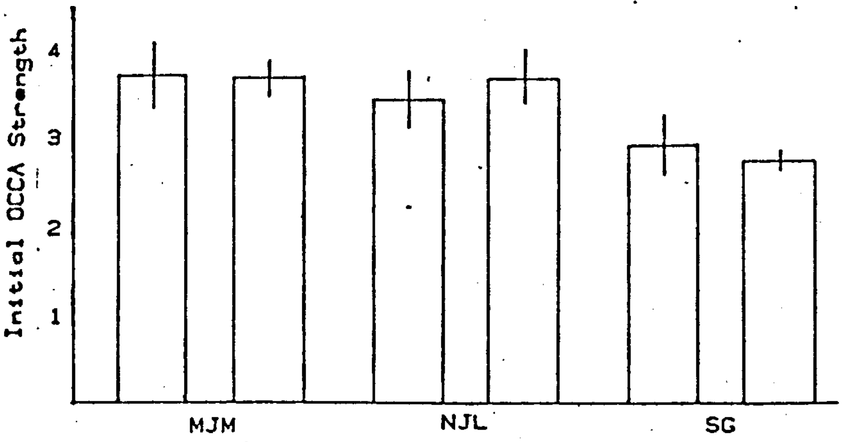
	Left Eye	Right Eye
Experiment 1	R///	G///
	G\\\	R\\\
Experiment 2	R///	R\\\
	G\\\	G///

The results for 3 amblyopic and 3 normal subjects are shown in Fig. 7.8. Experiment 1 refers to runs in which the gratings were the same and the colours different, and experiment 2 to those in which the colours were the same and the gratings different. The aftereffects were different in each eye, but as in each case they were complementary to the grating and colour pairings of the induction stimuli, they are all shown as positive. The results reveal that the type of binocular rivalry does not affect the strength of the McCollough effect in the amblyopic eye (shown cross-hatched) to a great extent, as under both conditions the strength of the aftereffect was low. However, the strength in the normal eyes was affected to a different extent by the two types of rivalry. When the colours were different and the grating orientation the same, the normal eye developed a large (in two cases, larger than average) McCollough effect. When the gratings were orthogonal and the colours were the same in each eye, smaller than average aftereffects developed in the normal eye (though they were larger than the OCCA in the amblyopic eye). Normal subjects, as expected, showed no asymmetry of results between the two eyes,

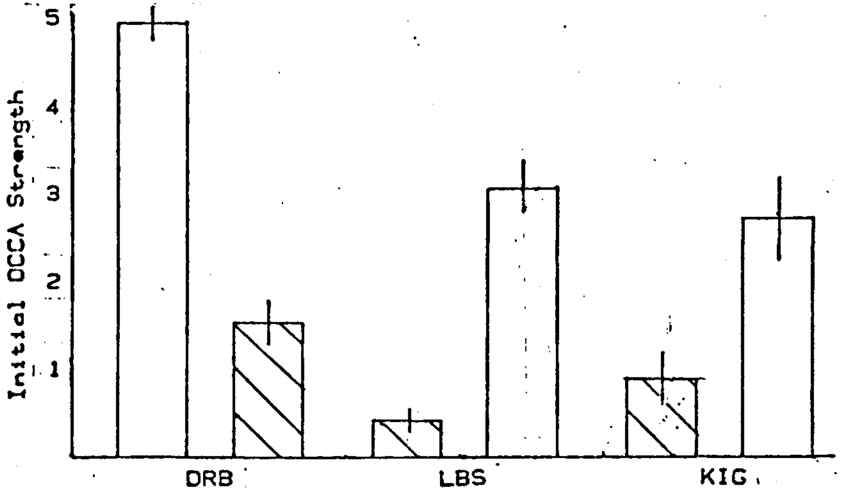
Fig. 7.8 Monocular test after binocular (rivalry) induction

Expt. 1. Gratings same orientation: colours different

Normal Subjects

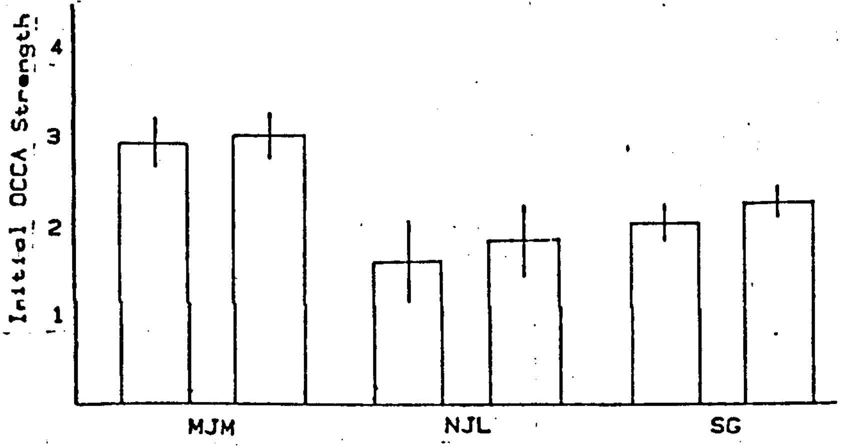


Amblyopic Subjects

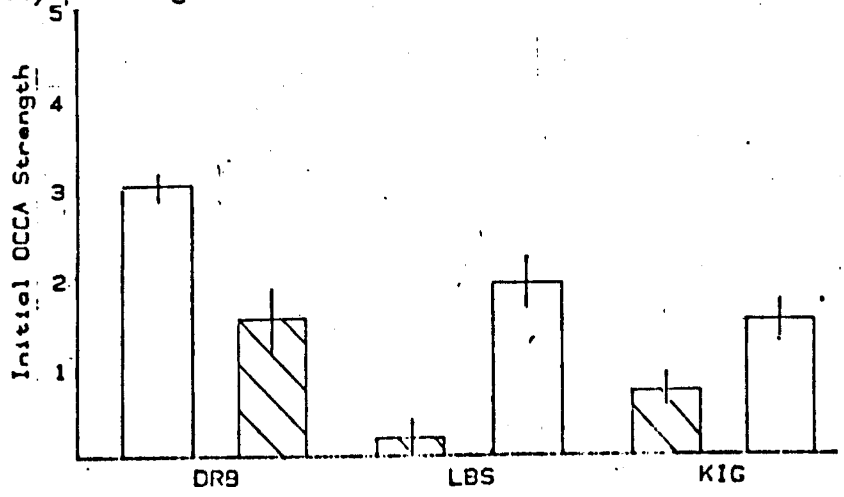


Expt. 2. Colours same: gratings different orientation

Normal Subjects



Amblyopic Subjects



but did show a greater OCCA in both when when the gratings were the the same orientation.

7.6. Dichoptic Stimulation

The experiments in this chapter have shown that amblyopic, and some stereoblind, subjects show different transfer properties from normal subjects. Following a suggestion by Dr. V. MacKay, it was decided to investigate the effect of amblyopia on dichoptic stimulation, since it has been demonstrated that in normal subjects, McCollough effects can be induced dichoptically (MacKay and MacKay, 1973a and 1975b). Aftereffects resulting from dichoptic stimuli must rely on some degree of interocular interaction.

Amblyopic and stereoblind subjects did a number of runs: half with the achromatic gratings presented to the amblyopic, or non-dominant, eye and the colour fields to the normal eye; and the other half with the reverse arrangement.

7.6.1. Initial Strength

MacKay and MacKay (1975b) have shown that dichoptic stimulation in most normal subjects results in a weak, normal McCollough effect in the colour stimulated eye and a stronger 'anomalous' McCollough effect in the grating-stimulated eye (i.e. colours same as original pairing). Since amblyopic and stereoblind show different transfer from one eye to the other, it was of interest to investigate whether varying the dichoptic stimuli presented to the two eyes resulted in different aftereffect strengths. The results for 3 amblyopic and 2 stereoblind observers are shown in Fig. 7.9. The cross-hatched data represent the amblyopic, or non-dominant, eye. Experiment 1 refers to runs when the gratings were presented to the normal eye and experiment 2 when coloured fields were presented to the normal eye.

The data show that all subjects develop large McCollough effects in each eye under both conditions; and, as in the data presented by MacKay and MacKay (1975b), the grating-stimulated eye generally developed a larger, anomalous OCCA. All the amblyopic and one stereoblind observer (MH), unlike normal subjects, developed different aftereffect strengths, dependent upon the direction of the dichoptic stimulation. These subjects developed a larger McCollough effect and a larger anomalous McCollough effect when the grating was presented to the normal eye.

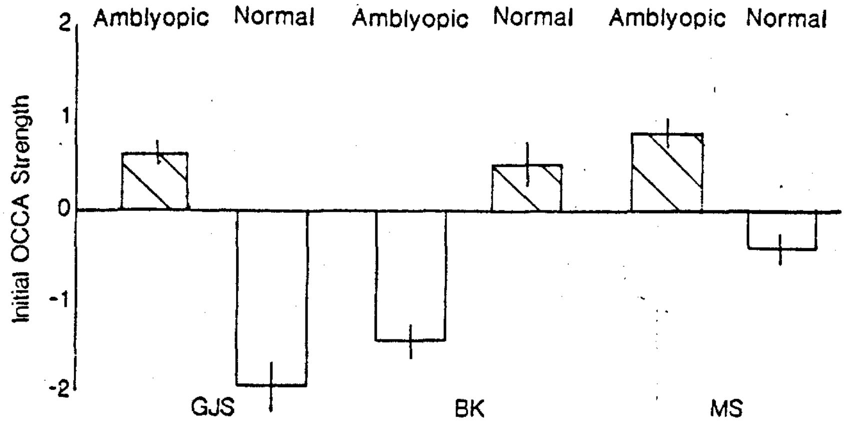
7.6.2. Decay of dichoptic aftereffects

The decay of dichoptically induced McCollough effects was studied by MacKay and MacKay (1975b), who reported that the time courses of both the normal and anomalous aftereffects were similar. Decay rates of dichoptically induced McCollough effects for 2 amblyopic and 1 stereoblind observer, are shown in Fig. 7.10. Both amblyopic and stereoblind observers, like normal subjects, show a similar decay rate for both the normal and anomalous McCollough effects.

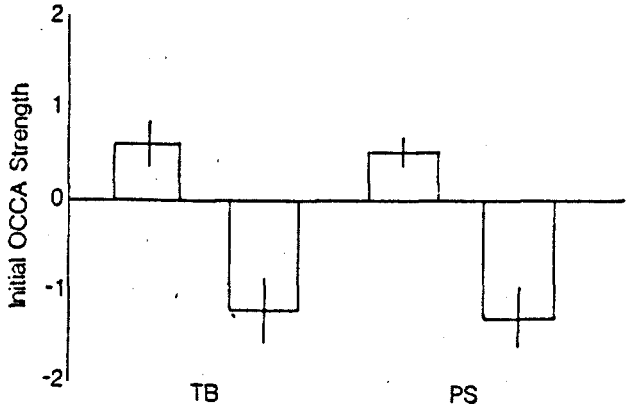
Fig. 7.9 Monocular test after dichoptic induction

Experiment 1: Grating presented to normal eye

Amblyopic subjects

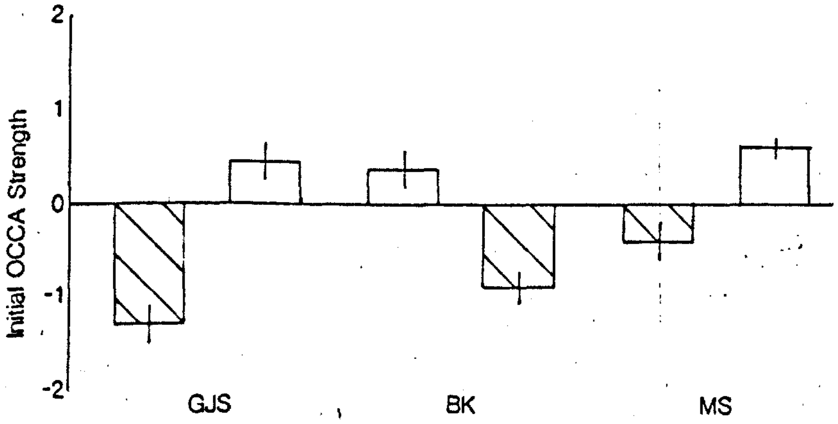


Stereoblind subjects



Experiment 2: Colour presented to normal eye

Amblyopic subjects



Stereoblind subjects

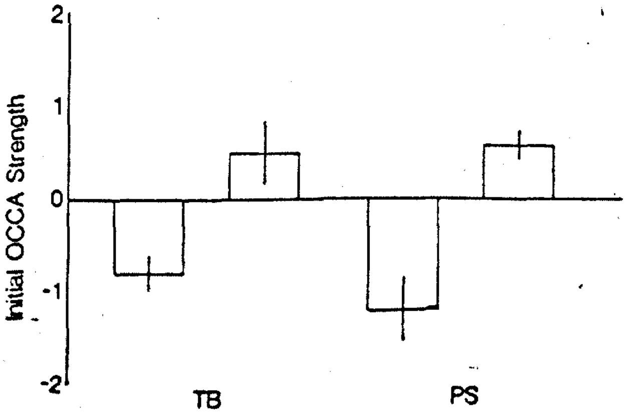
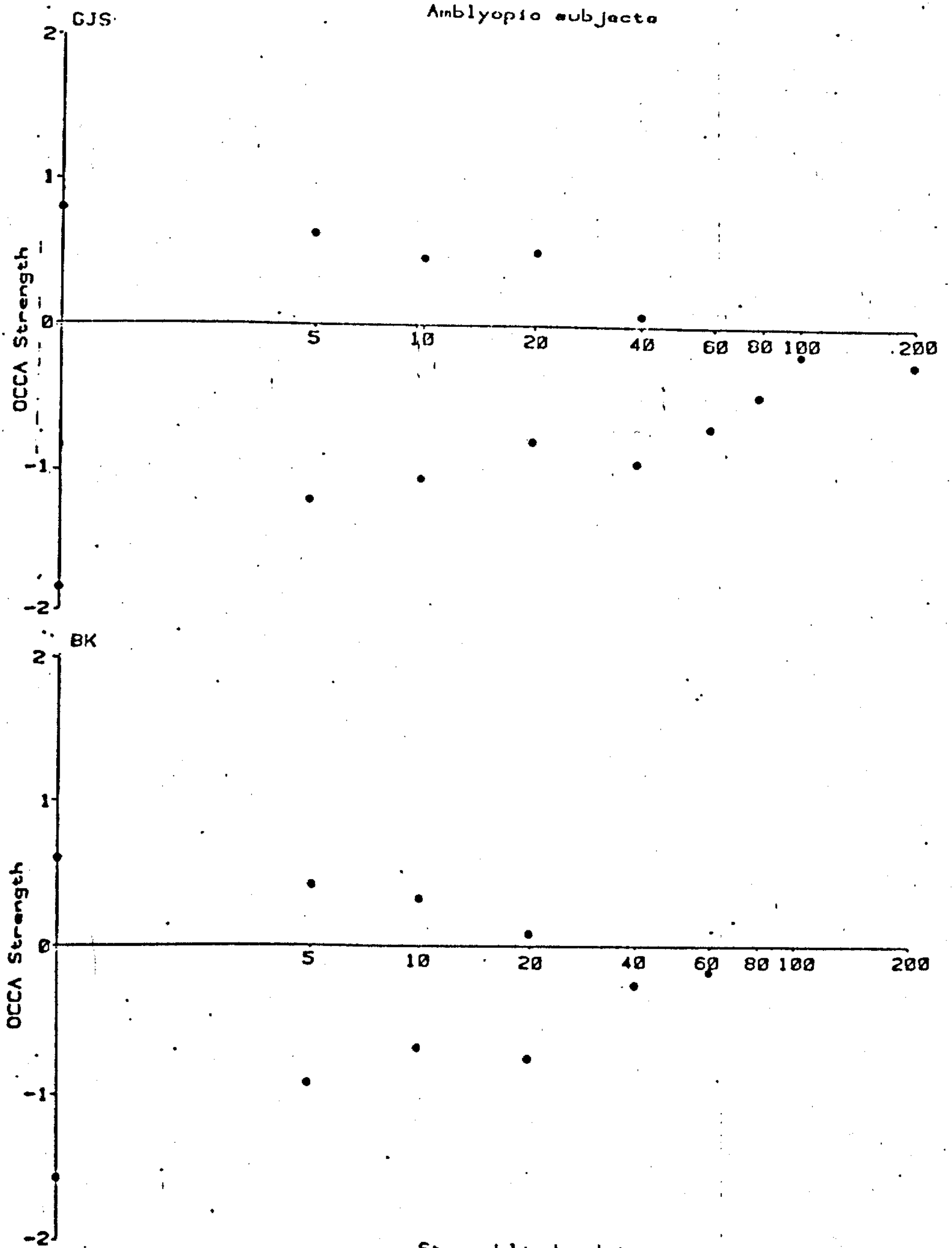
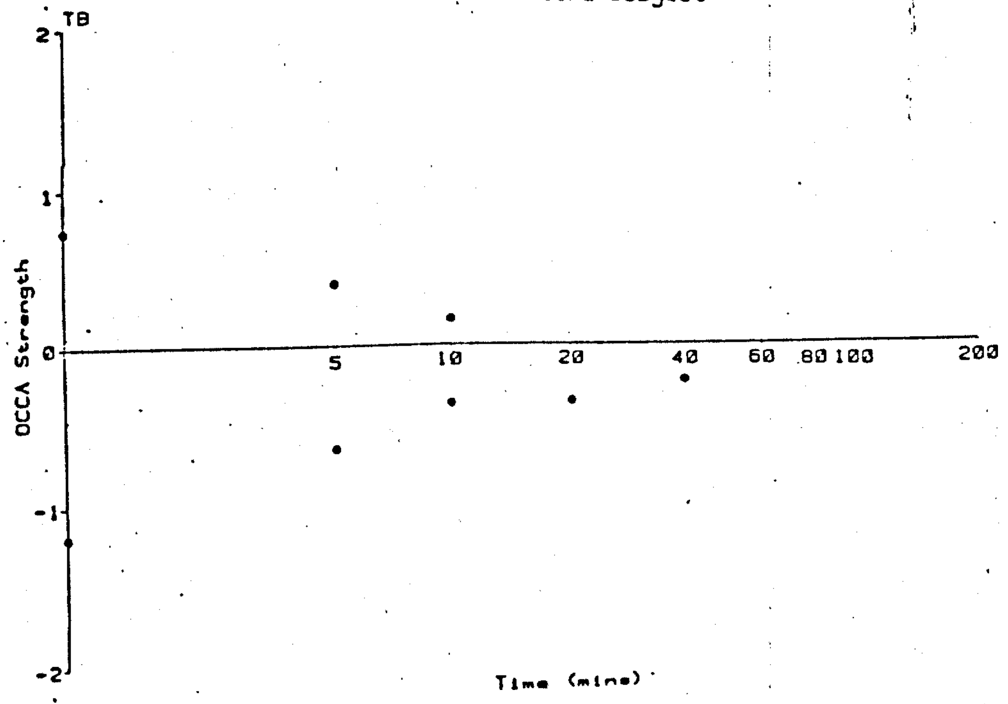


Fig. 7.10. Decay of dichoptic McCollough effects

Amblyopic subjects



Stereoblind subject



7.7. Conclusions and Discussion

The general conclusion which emerged from this chapter is that visual abnormalities may be one source of intersubject variability of the McCollough effect, particularly when studying interaction between the eyes. Unlike normal observers, amblyopic and some stereoblind subjects develop significantly different aftereffects in each eye after binocular induction. The amblyopic or non-dominant eye always developed a smaller OCCA strength after binocular induction but after monocular induction the strength in those eyes increased substantially. Past evidence has shown that amblyopic and stereoblind subjects have reduced interocular transfer of a variety of achromatic aftereffects (Ware and Mitchell, 1974). This data, together with that showing that the McCollough effect does not transfer to any great extent in normal subjects (Coltheart, 1973), suggested that amblyopic subjects would not exhibit transfer of the OCCA. However, amblyopic showed greater transfer (up to 50%) than normal subjects (less than 11%) but only from the amblyopic to the normal eye. After dichoptic induction, amblyopic subjects developed a larger McCollough effect and 'anomalous' McCollough effect when the gratings were presented to the normal eye than when gratings were presented to the amblyopic eye. Normal subjects show no such asymmetry. Finally, after binocular induction in which the inputs to the two eyes were different it was found that amblyopic observers developed a much larger OCCA strength in the normal eye when the gratings were the same orientation and the colours different than when the colours were the same and the gratings were different orientations. The amblyopic eye was unaffected. Normal subjects showed no asymmetry between the two eyes but did develop a larger OCCA in both when the gratings were the same orientation.

Apart from revealing a source of variability the experiments of this chapter have raised some interesting points. It is generally believed that the poor stereopsis of both amblyopic and stereoblind individuals is caused by a lack of binocularly driven neurones (Hohmann and Creutzfeldt, 1975; Mitchell et. al., 1973) and the reduction in interocular transfer of some achromatic aftereffects is taken as evidence of this. It is interesting therefore that such subjects show greater transfer of the McCollough effect than normal subjects. MacKay (1978) has suggested that the McCollough effect may not be cortical, as is widely believed, but may be located at a relatively unsophisticated level of the visual system, possibly at the lateral geniculate nucleus. The experiments showing that stereoblind and amblyopic subjects have enhanced transfer of the OCCA and those showing that they develop dichoptic aftereffects, if such subjects are deficient in binocular neurones, strengthens this possibility.

CHAPTER 8 EFFECTS OF VISUAL STIMULATION UPON DECAY

8.1 Introduction

One of the most intriguing aspects of the McCollough effect is its persistence, which has stimulated much research and theoretical debate. Most investigators have reported that the aftereffect can be detected for at least 2 or 3 days (MacKay and MacKay, 1973b; Stromeyer, 1971) and some have claimed that it may last up to 2 weeks, if subjects are not exposed to test gratings (Jones and Holding, 1975). The rate of decay of the OCCA has been found to follow a characteristic time course which was approximately linear on either log/log scales (MacKay and MacKay, 1973b) or linear/log scales (Riggs, White and Eimas, 1974) in normal room illumination. Various reports have shown that variation of the visual stimulation after induction changes the decay rate. At one extreme, MacKay and MacKay (1975a, 1977b) found that darkness completely arrests the decay of the OCCA and that readings taken after may even be higher than readings taken before a period of darkness. Skowbo et. al. (1974) on the other hand, reported that complete darkness was associated with a slow decay which was similar to the decay caused by homogeneous chromatic fields and 'natural' visual stimulation, but exposure to achromatic gratings (of the same orientation and spatial frequency as the induction gratings) caused a marked fading of the aftereffect. Subsequent reports have confirmed the latter observation and have indicated that longer exposure to achromatic gratings and high luminance gratings produces a greater decline of the McCollough effect than short exposures or low luminance gratings (Skowbo and Clynes, 1977; Skowbo, 1979).

Past evidence, therefore, indicates that although there is agreement about the effects of achromatic gratings upon the decay rate of the McCollough effect, the effects of other visual parameters are not clearly defined.

The experiments reported in Chapter 4 showed a large degree of inter and intrasubject variability of the decay rate. This variability occurred despite attempts to keep the experimental conditions constant. Subjects remained in a room of constant luminance while decay measurements were taken and were asked not to consume any food, coffee or nicotine. In general these instructions were obeyed for at least 100mins. after induction but these precautions did not reduce the variability to a great extent. Although the overall luminance level of the laboratory was constant, some aspects of the visual stimulation could not be controlled. Subjects were exposed to contrast edges within the laboratory which changed according to the direction of their gaze. Furthermore, since some subjects wrote or drew during the decay process they were exposed to varying densities and orientations of lines. Some subjects may have been exposed to a lowered luminance level if they closed their eyes owing to tiredness or boredom. Finally, since both subjects and experimenters' clothes varied from experiment to experiment (sometimes patterned, sometimes plain) subjects would have been exposed to differing chromatic stimulation.

The experiments reported in this chapter were performed to clarify some of the past evidence and to examine any aspects of the post-induction visual stimulation which may have affected the decay rate.

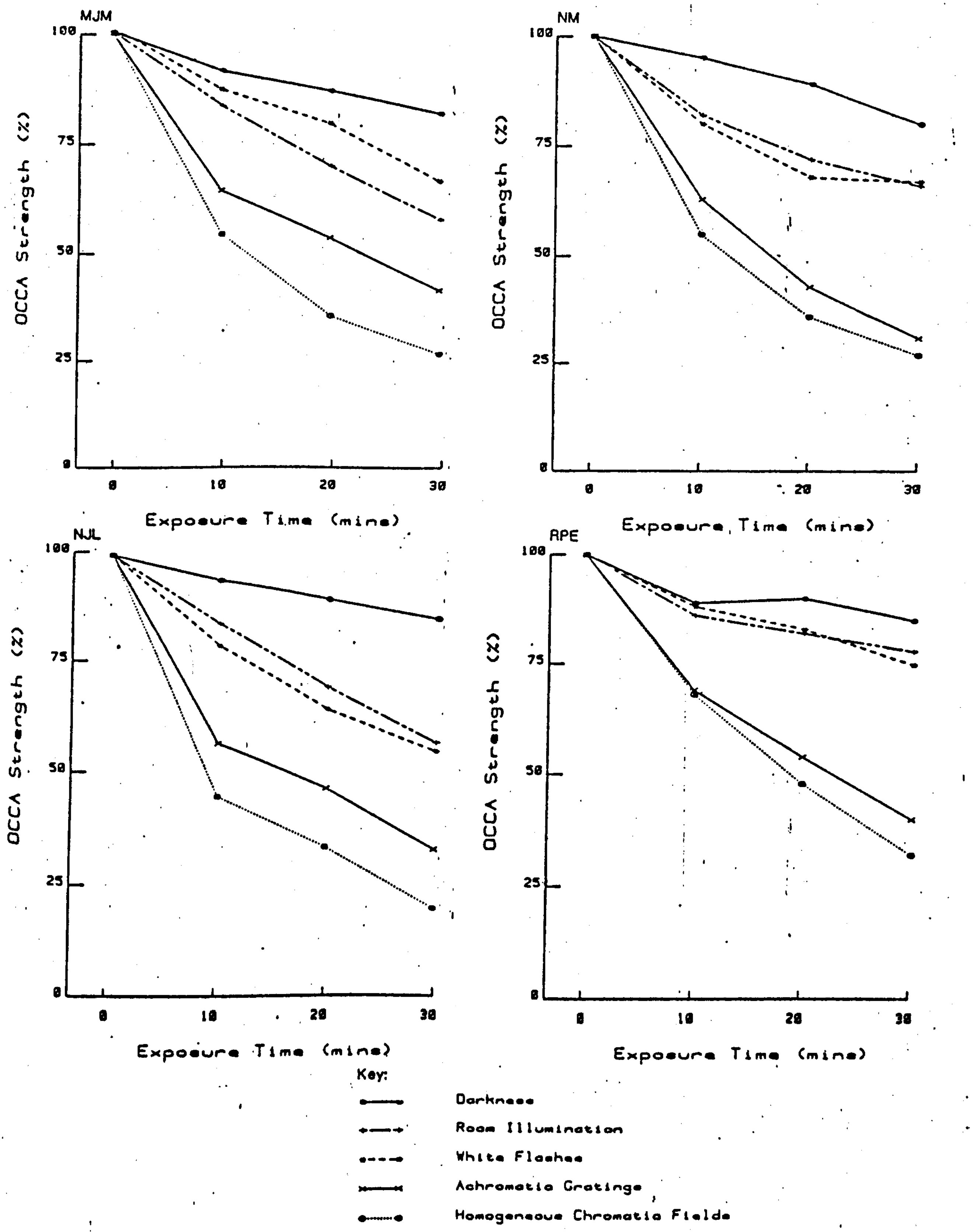
8.2 Monocular Experiments

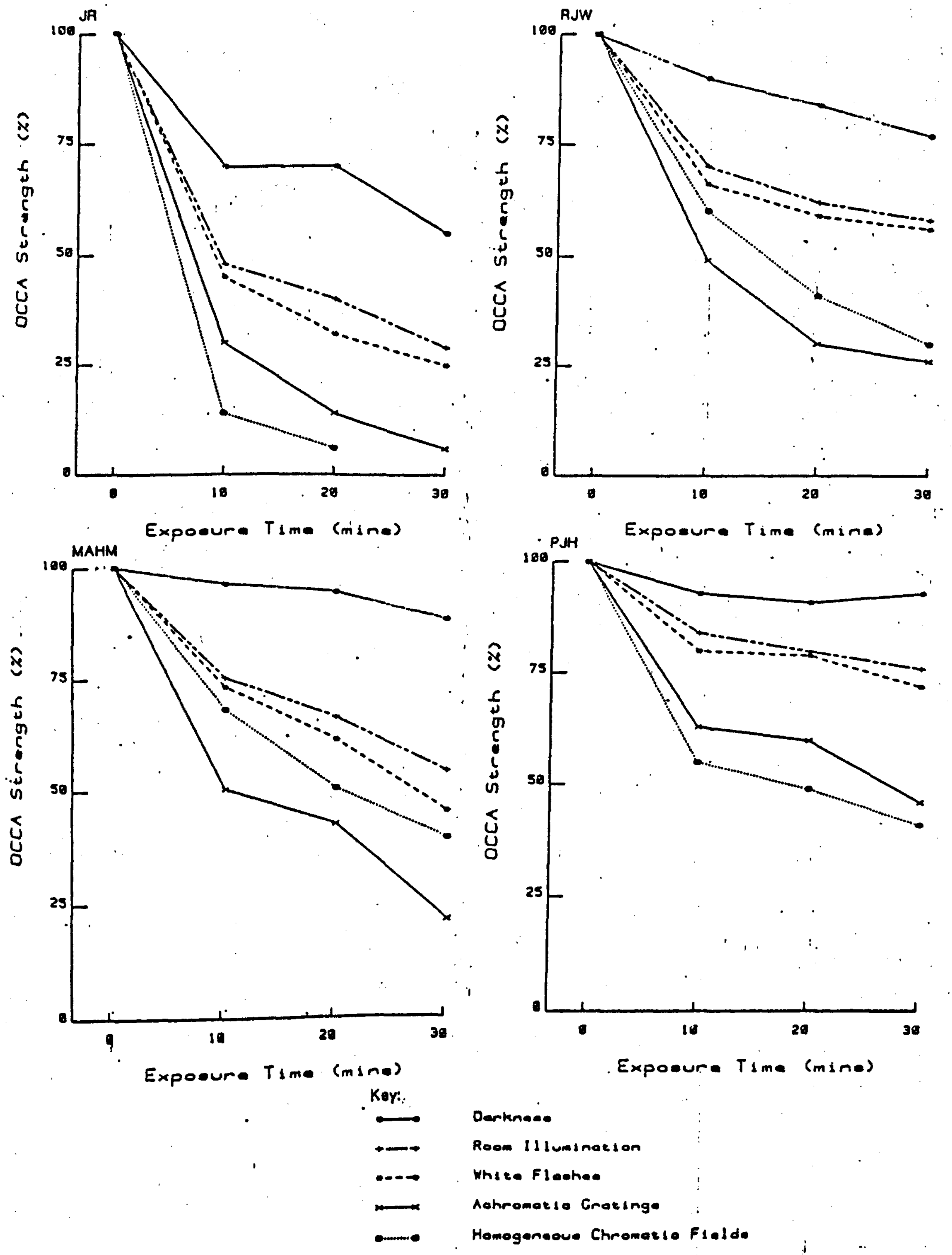
The experiments reported in this section are to some extent repeats of the experiments of Skowbo et.al. (1974). Both the induction stimuli and post-induction stimuli were presented monocularly. Five types of post-induction stimuli were used:

1. Darkness
2. Room illumination
3. White fields
4. Alternating orthogonal achromatic gratings (of the same orientation and spatial frequency as the induction gratings)
5. Alternating red and green homogeneous fields

Stimuli 4. and 5. were presented tachistoscopically for 5 s. each with no dark intervals; stimuli 3 were presented for 4s. with a 1s. 'off' interval. The luminances of stimuli 3,4, and 5 were approximately matched. The induction stimuli were presented for 1s. with a 4 s. 'off' interval. In this respect the experiment varied slightly from that of Skowbo et.al., who used alternating 5s. stimuli for both the induction and post-induction stimuli. The OCCA was measured within 10-15s of the end of induction. The results averaged over 2 runs, for 8 subjects, are shown in Fig. 8.1. Since all the decays started at slightly different initial strengths (because they represent runs performed on separate occasions) the decays are presented as a percentage of the aftereffect recorded just after induction (i.e. 0 mins. of decay).

Fig. 8.1 Effects of visual stimuli upon the decay of the McCollough Effect



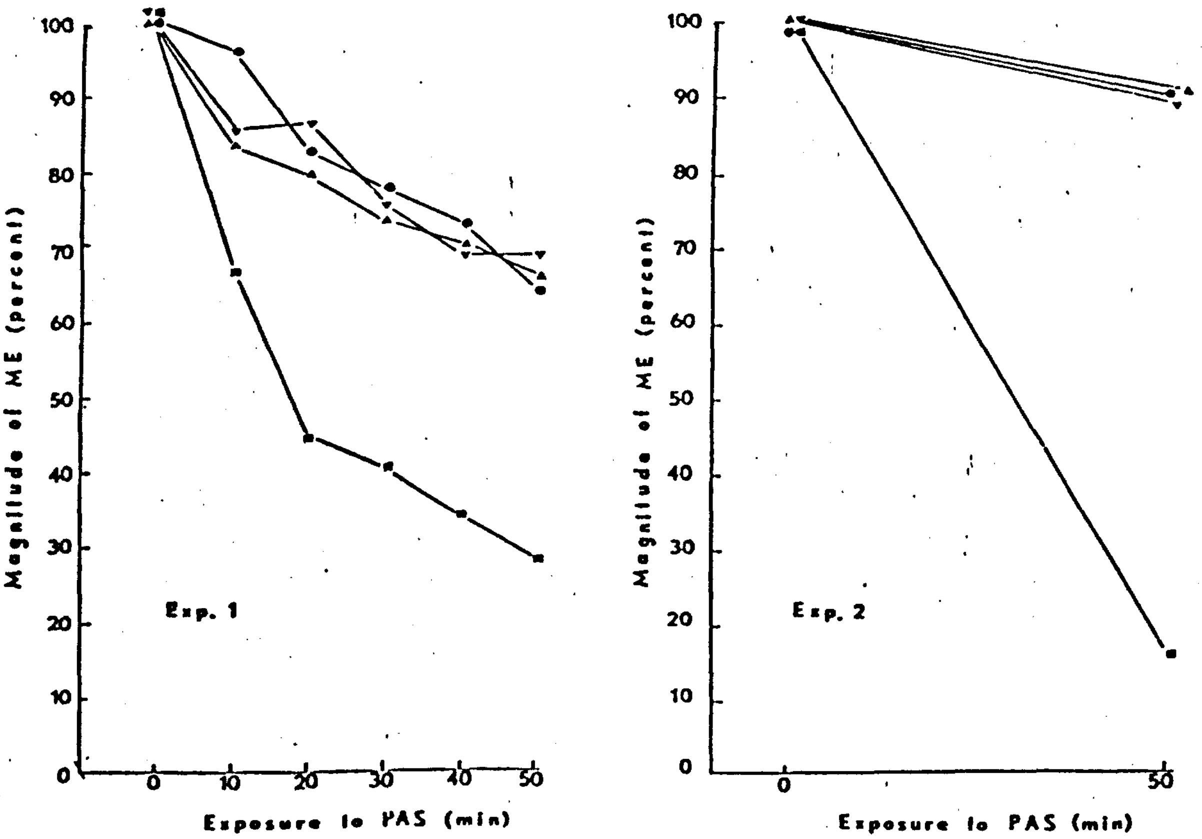

JR
RJW
MAHM
PJH
OCCA Strength (%)
100
75
50
25
0
0
10
20
30
Exposure Time (mins)
Key:
Darkness
Room Illumination
White Flashes
Achromatic Gratings
Homogeneous Chromatic Fields

The results show that, as predicted by past research, achromatic gratings produced a rapid decay of the aftereffect. The most rapid decay, however, was associated with the homogeneous chromatic fields in all but two subjects (MAHM & RJW). The darkness condition always produced the least decay; room illumination and alternating white fields were associated with a medium decay rate between the two extremes. It might be postulated that the achromatic gratings cause a fast decay because they are effectively test patterns and the aftereffect seen on such patterns, being opposite to the colours seen during adaptation, acts as a neutralizing stimulus. Skowbo et. al. (1974) used two points to argue against such a theory and these are relevant to the results reported here. Firstly, aftereffects are best seen on test patterns where the orthogonal gratings are presented side by side; but the gratings shown during decay were alternated and as a result subjects reported that the gratings were achromatic. Secondly, McCollough effects are best seen on gratings of low photopic luminance; but the luminance of the achromatic gratings was much higher than that of the test gratings. Since subjects did not see the aftereffect on the achromatic gratings the neutralizing effect would have been negligible.

Some of the results contrast sharply with those of Skowbo et.al. (1974) who found rapid decay <u>only</u> with achromatic gratings and about the same (slower) decay with darkness, 'natural' visual stimuli and homogeneous chromatic fields (see Fig. 8.2). The discrepancies in the two sets of results are difficult to explain, though the differences in experimental procedure may have had an influence. After all the experiments reported in this thesis, the OCCA was allowed to decay naturally (between 2 to 7 days, depending upon the pre-test readings) whereas Skowbo et.al 'neutralized' any remaining aftereffects after each session by presenting opposite filter-grating combinations to those used during induction. White (1976) has shown that such neutralization (or nullification) processes do not truly eliminate the OCCA and that both the original and neutralizing McCollough effect may be retained. Skowbo et.al. (1974) reported that at least 24hrs. elapsed between sessions; but if the stimulating conditions were not presented in random order, the previous day's McCollough effect (either 'inducing' or 'neutralizing') may have systematically influenced the results. Furthermore, after each test procedure, Skowbo et.al. exposed subjects to homogeneous fields for 7 mins., which could introduce complications in the decay measurements.

Fig. 8.2.

From- SKOWBO, GENTRY, TIMNEY, AND MORANT (1974)



Figs. 1 and 2. Influence of PAS conditions on decay of the ME. The ordinate is the percentage of the ME measured before PAS which remains after PAS. The abscissa is the amount of time of exposure to PAS. In Experiment 1, there were five 10-min segments of PAS; in Experiment 2, PAS was continuous for 50 min. The PAS conditions are represented by the symbols ■———■ for achromatic gratings, ▼———▼ for homogeneous chromatic fields, ▲———▲ for natural visual stimulation, and ●———● for complete darkness.

The results shown in Fig. 8.1 which indicate that darkness was associated with very little decay of the OCCA, are very similar to those of MacKay and MacKay (1974a, 1975a and 1977b) who found no decay at all if subjects were kept in complete darkness after induction. The slight decay reported in this thesis may have been caused by the repeated testing at 0, 10 and 20 mins. since the test procedure has been shown to cause some decay (Jones and Holding, 1974).

8.3 Dichoptic comparisons of the effects of visual stimuli

The preliminary experiments reported in Chapter 4 revealed that both the initial strength and the decay rate of the McCollough effect showed considerable intrasubject variability on different occasions. It was, therefore, possible that some of the results reported above were not truly representative, since each decay was measured on a separate occasion and may have been influenced by day to day variability. The preliminary experiments also showed that following binocular induction, the initial strength and decay rate were always very similar in each eye. This observation presented an ideal way of comparing the effects of two stimulating conditions in a controlled manner. Some of the above stimulating conditions were, therefore, repeated after binocular induction, and the decay rates of the left and right eyes were compared. In each section the results presented are the average of 2 runs; the first when stimulus A was presented to the left eye and stimulus B to the right; and the second when stimulus B was presented to the left eye and stimulus A to the right. Any biases produced by a dominant eye were therefore removed. The laboratory was darkened during the stimulus presentation to prevent interference from extraneous light. The experimental procedure was, in all other respects, the same as that of Section 8.2. Apart from the darkness condition all the stimuli were approximately matched for luminance.

8.3.1 Comparison of homogeneous chromatic fields with darkness

In this experiment the red and green homogeneous fields were projected in the tachistoscope and the darkness condition was produced by a light-tight patch over one eye. A comparison of the two decay rates appears in Fig. 8.3 and, in common with the earlier experiments, it shows that red and green homogeneous fields produced a marked decrease in the strength of the McCollough effect whereas darkness was associated with very little (maximum of 14%) decay. However, this comparison does not reveal whether the chromatic stimulation or the difference in luminance affected the decay rate.

8.3.2 Comparison of achromatic gratings with darkness

Darkness was again produced in one eye by using a light-tight patch and the gratings were presented using the tachistoscope. The results (shown in Fig 8.4) indicate that achromatic gratings were associated with a rapid decay of the OCCA when compared with darkness; but as the luminances were different it was not clear whether the rapid decay was caused by the patterned stimuli or the increased luminance of the grating stimuli.

Fig. 8.3. Comparison of red/green fields with darkness

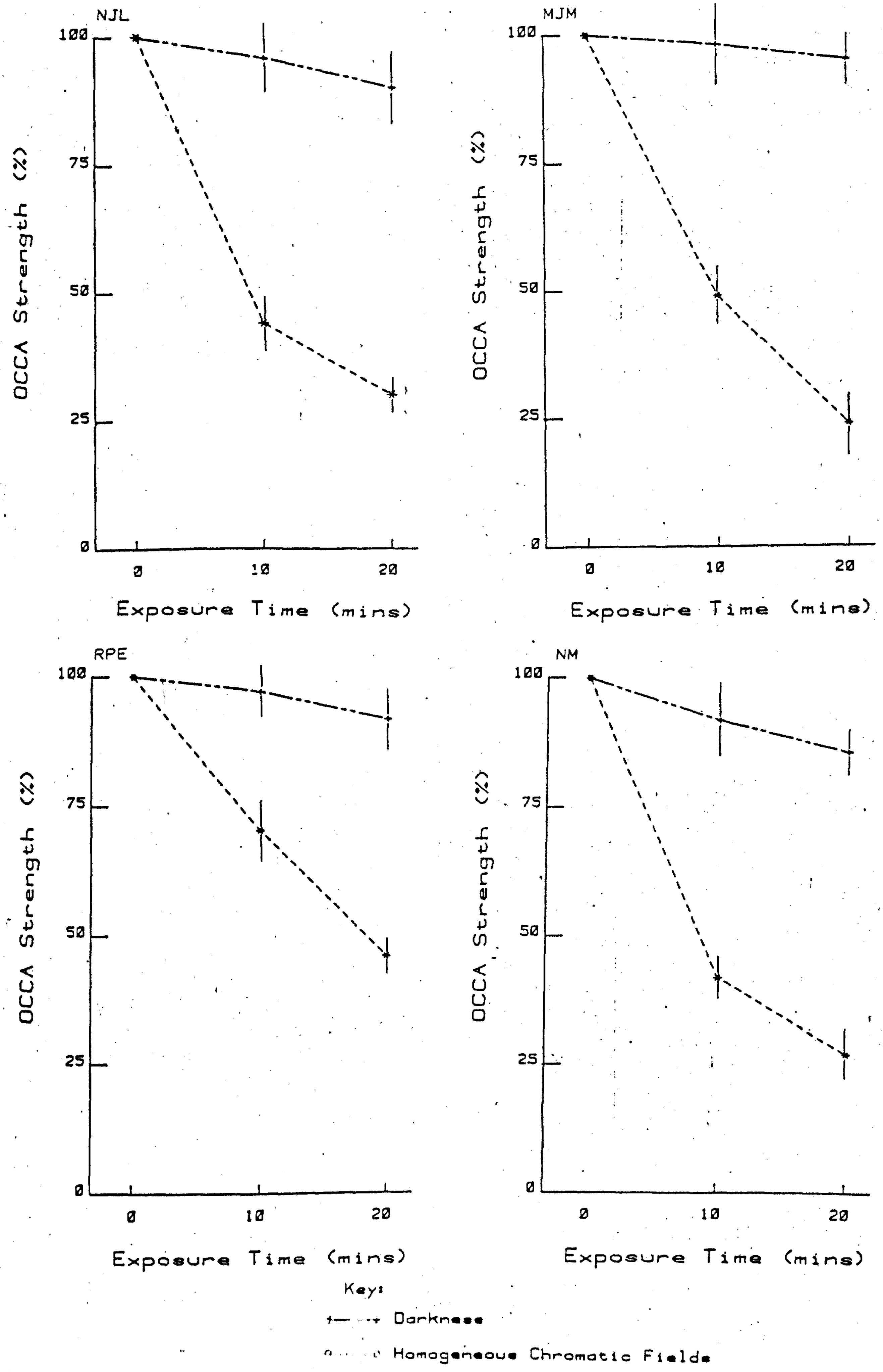
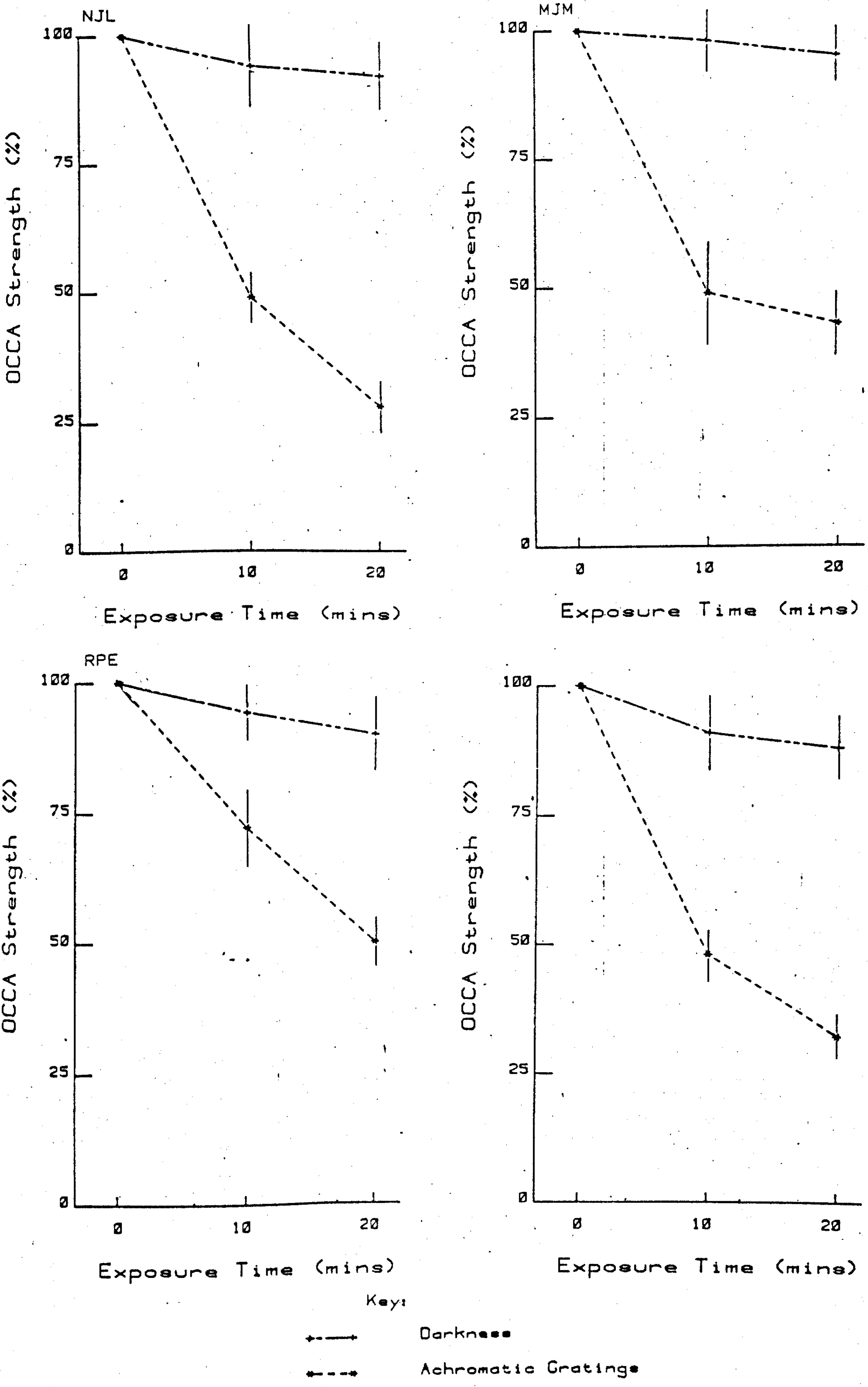


Fig. 8.4. Comparison of achromatic gratings with darkness



8.3.3 Comparison of homogeneous chromatic fields with achromatic gratings

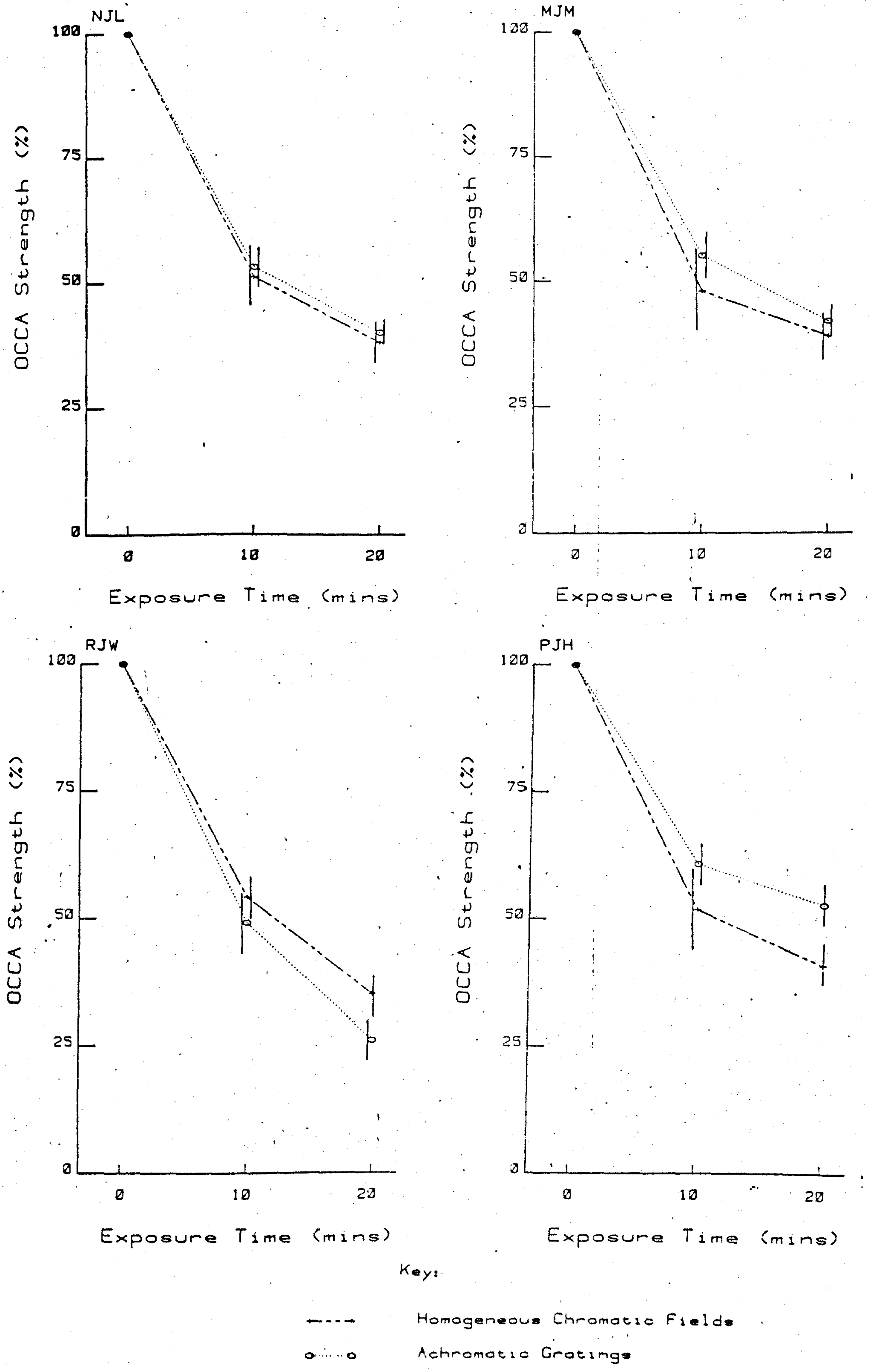
Controlled comparisons of the effects of homogeneous chromatic fields and achromatic gratings upon the decay of the McCollough effect were complicated because it is known that aftereffects can be induced dichoptically when chromatic fields are presented to one eye and gratings to the other. (MacKay and MacKay, 1973a and 1975b). In order to avoid dichoptic effects, a device was incorporated into the tachistoscope which changed the dichoptic colour and orientation pairings every 4 flashes. This arrangement should have had the effect of neutralizing any dichoptic aftereffects because small, opposite effects were repeatedly induced.

The results (Fig. 8.5) show that both stimulating conditions caused a marked decay of the OCCA but that the coloured fields were usually slightly more effective, even under the controlled conditions. However, neither condition shows the same degree of decrease for each subject as in the original experiments. These averaged results do not reveal the variability in each decay reading and in the results from run to run which may have resulted from the experiment conditions.

8.3.4 Comparisons of homogeneous chromatic fields with achromatic gratings: alternating fields

The variability of the results of Section 8.3.3 may have been due to the dichoptic interaction between the gratings and the coloured fields. Although the dichoptic 'pairing' of stimuli was

Fig. 8.5. Comparison of red/green fields with achromatic gratings



changed every 4 presentations to neutralize the dichoptic aftereffects, White (1977) has shown that such neutralization procedures do not remove the OCCA's but rather leave two separate McCollough effects. An alternative experimental procedure was used to compare the effects of the stimuli without dichoptic interaction. This procedure involved presenting the stimuli for 5s. with a 5s. 'off' interval. The coloured fields were presented to one eye during the off interval of the grating cycle and the gratings were presented to the other eye during the off interval of the coloured field cycle, i.e:

Time	1st Eye	2nd Eye
5s	R	off
10s	off	///
15s	G	off
20s	off	\\\

The results (Fig. 8.6) show a similar trend to those of Fig. 8.5, but each subject shows a greater decrease for each condition, even though the stimuli were presented for a shorter period during each 10min. presentation because of the increased 'off' time. These results were also less variable than those of Section 8.3.3 but the diagram does not show this.

8.3.5 Comparison of darkness with white fields

When the effect of darkness and white fields upon the decay were compared (Fig. 8.7) it was found that the decay caused by the white fields was much larger. Darkness, as in the previous experiments produced very little decay. Since both stimuli conditions varied in luminance only, the large decay caused by

Fig. 8.6. Comparison of red/green fields with achromatic gratings: alternating fields

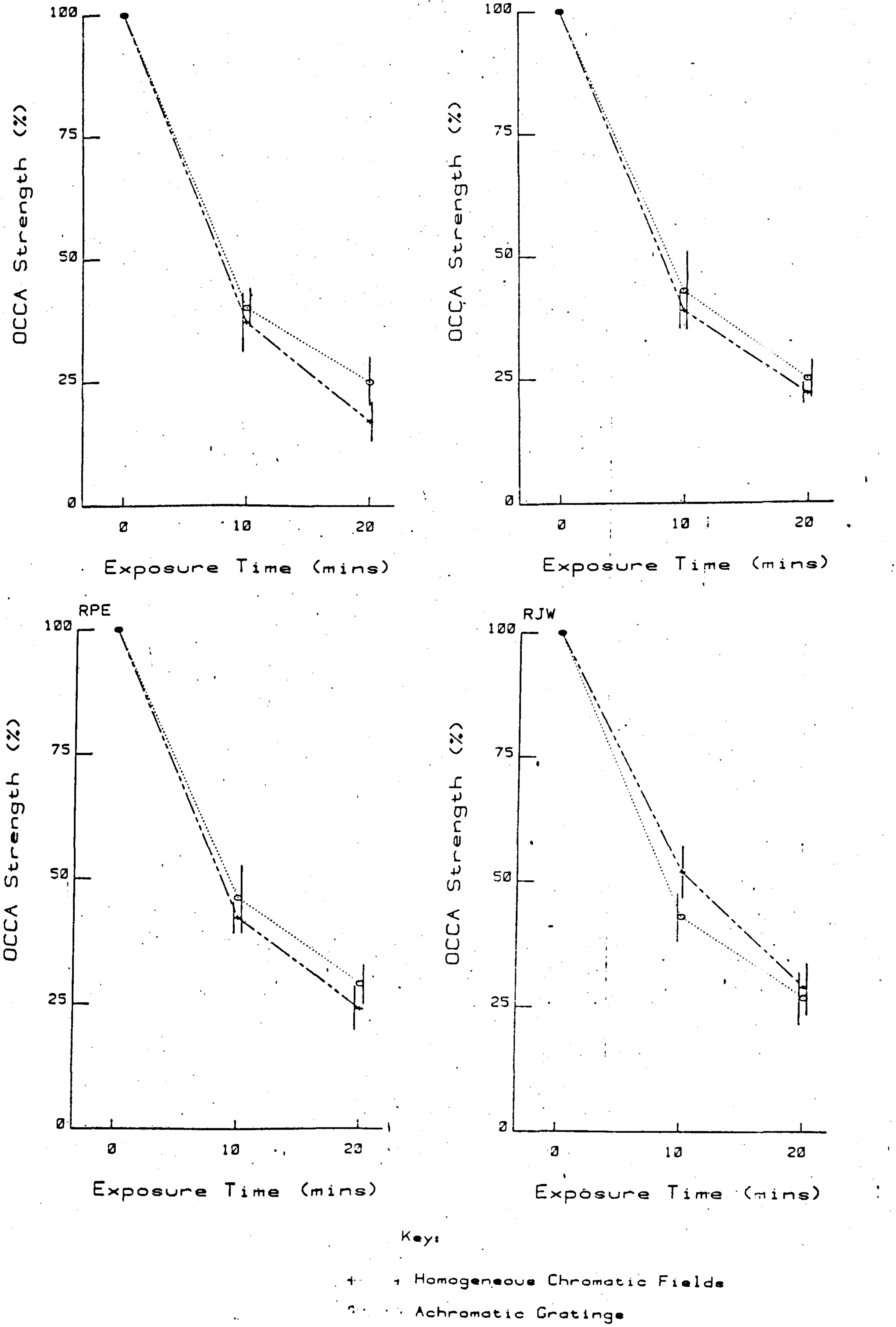
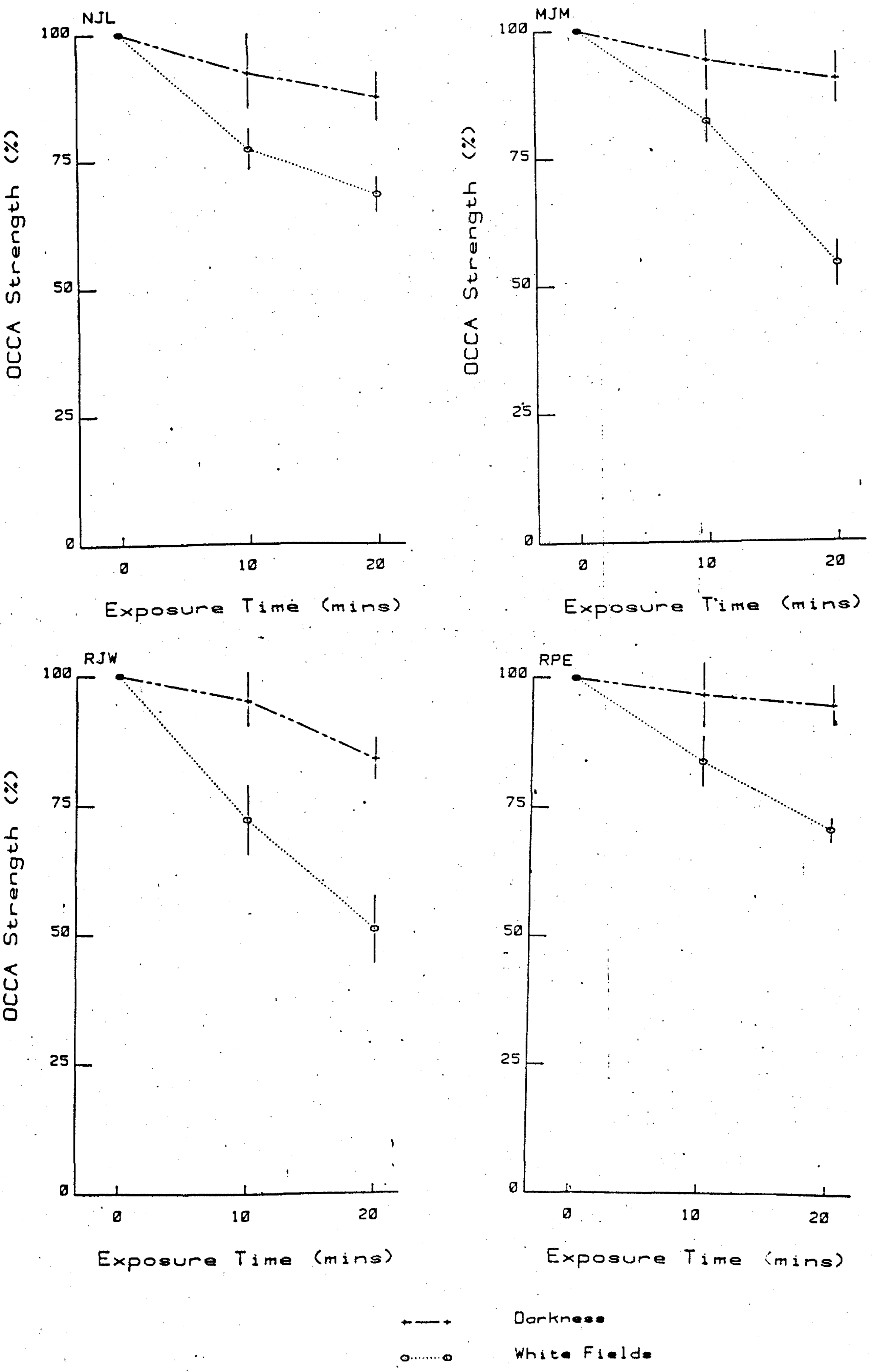


Fig. 8.7. Comparison of white fields with darkness.



achromatic gratings and homogeneous chromatic fields as compared to darkness may have been due to luminance difference.

8.3.6 Comparison of homogeneous chromatic fields with white fields

In this experiment the stimuli were presented simultaneously to either eye. The results (Fig. 8.8) show that the red and green fields produced a much more rapid decay than the white fields, even though they were approximately matched in luminance. This indicates that the McCollough effect was affected by the chromatic stimulation rather than the luminance of the red and green fields.

8.3.7 Comparison of achromatic gratings with white fields

The effect of achromatic gratings was compared with the effect of white fields using simultaneous dichoptic presentations, and the decays are shown in Fig. 8.9. These reveal that the gratings reduced the strength of the OCCA to a much larger extent than the white fields. Since they were approximately matched for luminance this suggests that the patterned stimuli rather than the luminance of the fields was responsible for the rapid decay of the aftereffect.

8.3.8 Summary of results

The dichoptic comparison of this section has consistently supported the data presented in Section 8.2. In all the experiments, darkness produced less decay than any other stimuli which were used. All the other stimuli had approximately the same

Fig. 8.8. Comparison of white fields with red/green fields

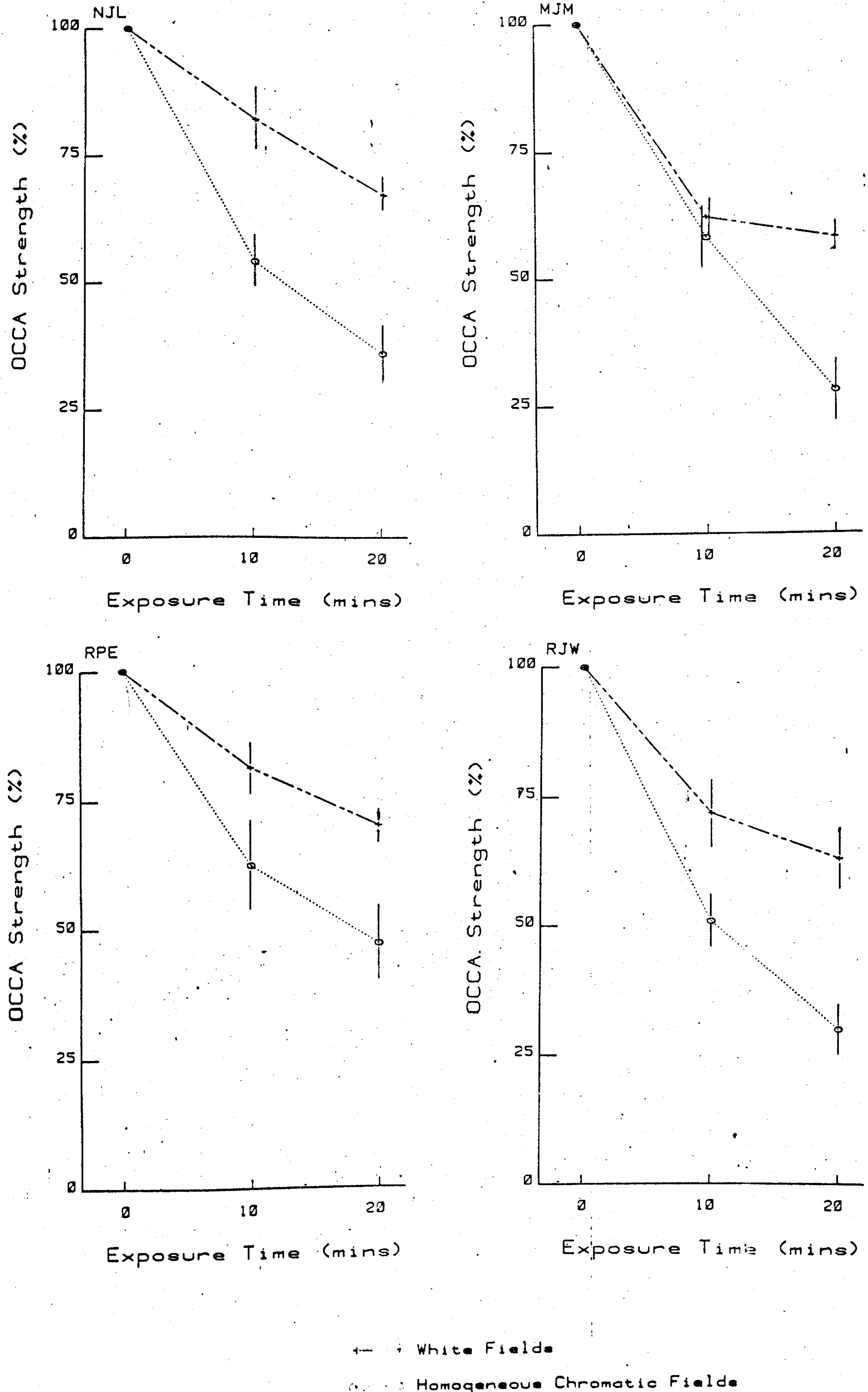
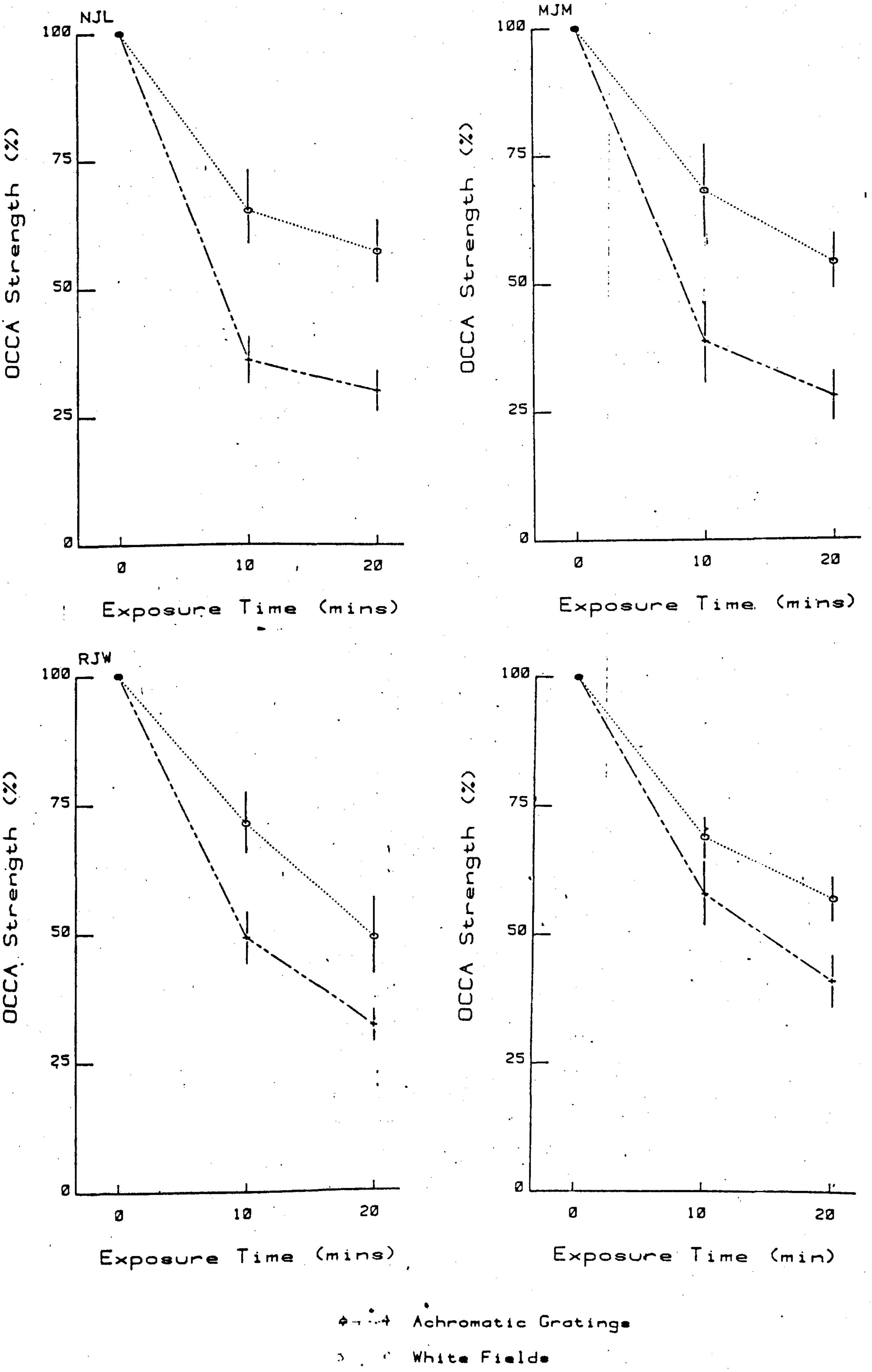


Fig. 8.9. Comparison of white fields with achromatic gratings



luminance. These findings are in line with past research which has shown that darkness produces little or no decay of the McCollough effect (MacKay & MacKay, 1977b). The other experiments have shown not merely that greater decay was associated with high luminance, but that a larger decay was caused by chromatic or patterned stimuli which were the same as those used during induction. In general, the homogeneous chromatic stimuli produced greater decay than the achromatic gratings, but the difference was slight. The one exception was subject RJW who, as in Section 8.2, showed slightly greater decay when stimulated with gratings.

8.4 Investigation of the effects of other chromatic and patterned stimuli upon the decay

In all the experiments reported so far in this chapter the chromatic and patterned stimuli have been identical to those of the induction stimuli. Further experiments were therefore performed to investigate whether any other chromatic or patterned stimuli, different from those used during induction, would have the same effect upon the decay of the OCCA. The experimental procedure was the same as that used in Section 8.3.

8.4.1 Comparison of red/green with blue/orange homogeneous fields

The coloured fields used in this experiment were the same size (12°x12° angular subtense at the eye) and were approximately matched for luminance. The red and green filters were the same as those used to induce the McCollough effect (see Chapter 3) and the blue and orange filters were 'Cinemoid' 19 and Kodak 558/13 filters respectively. The results (Fig 8.10a) show that both sets of

Fig. 8.10a. Comparison of red/green with blue/orange homogeneous fields

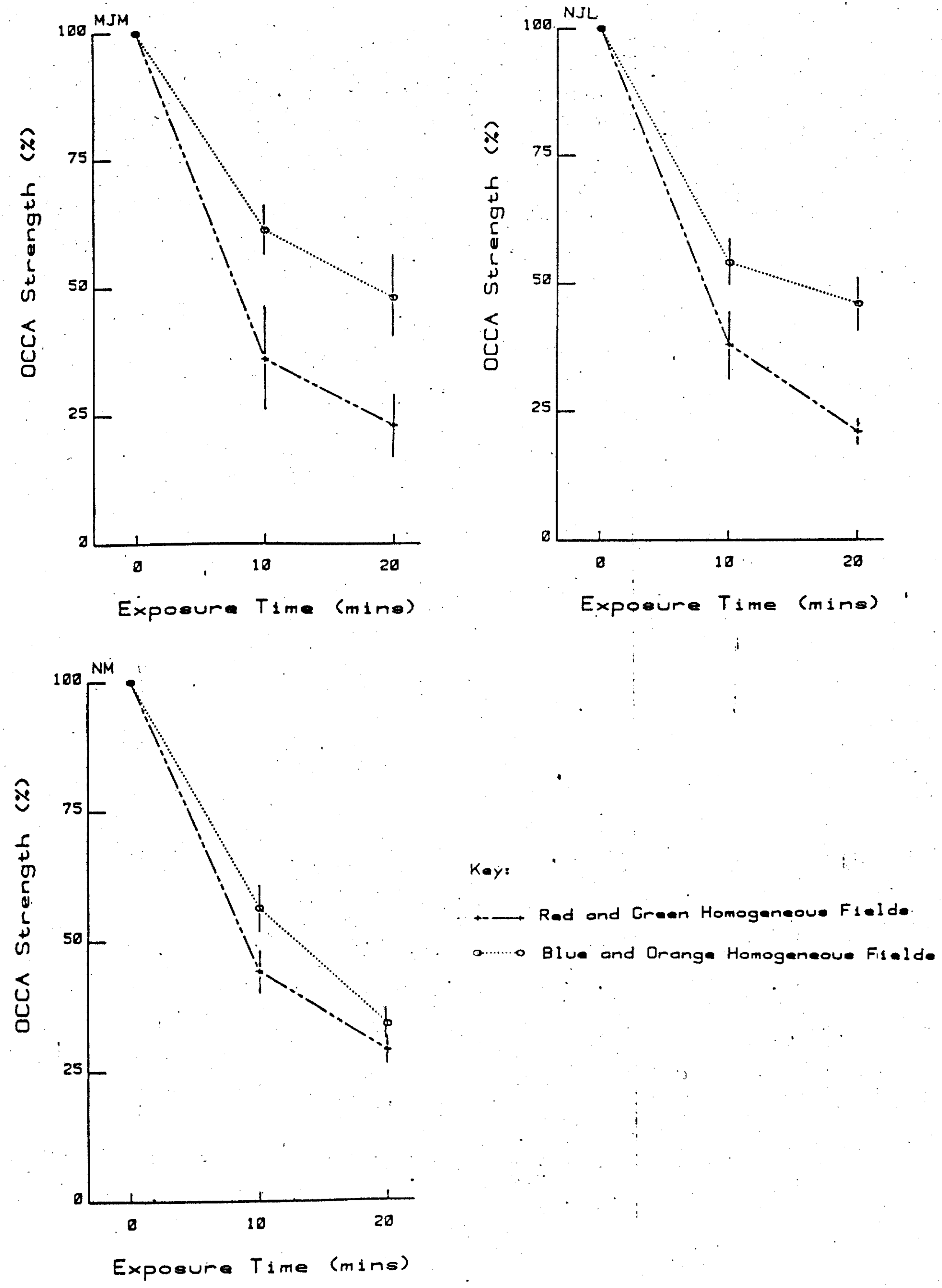
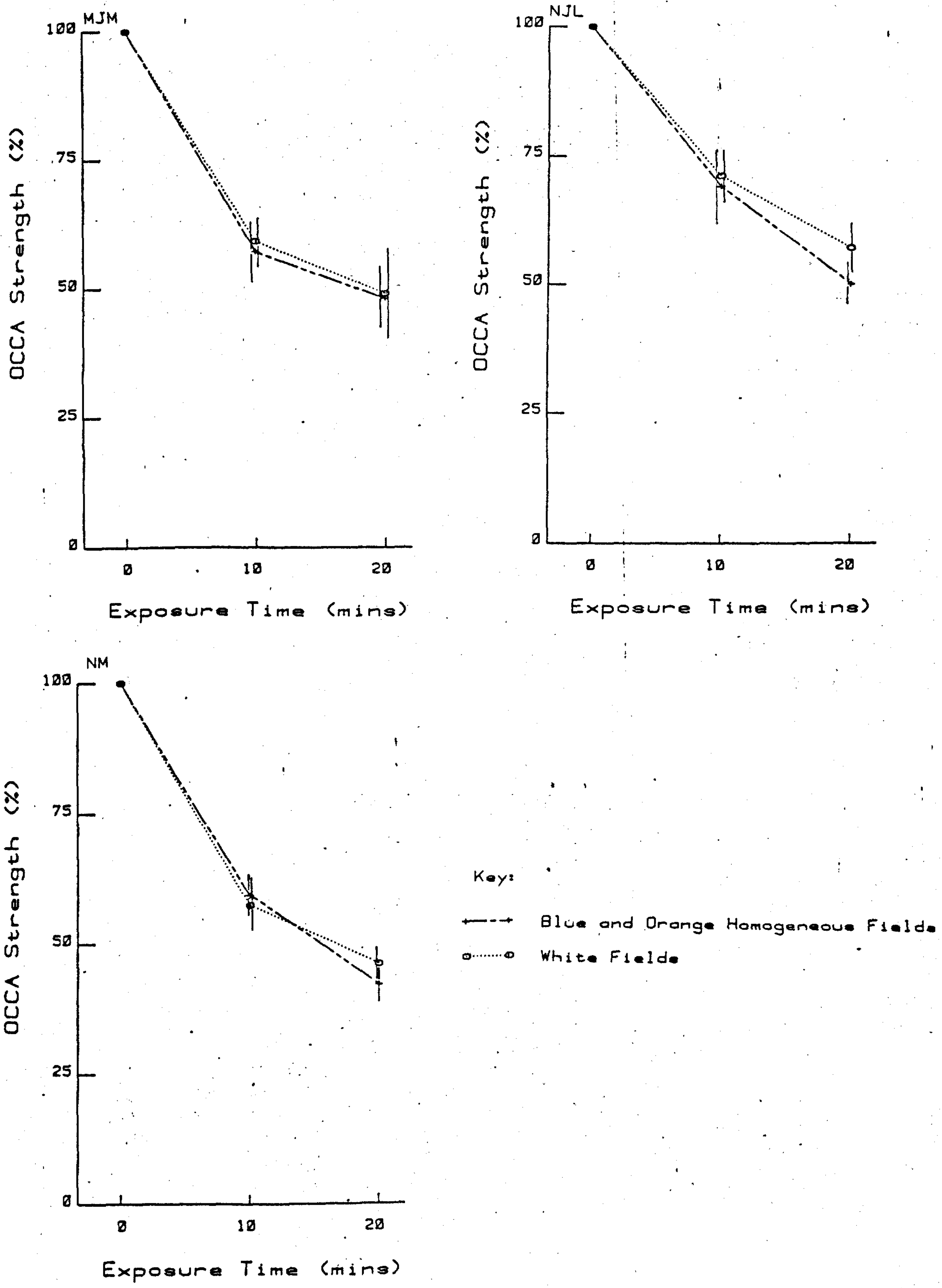


Fig. 8.10b. Comparison of blue/orange with white homogeneous fields.



homogeneous chromatic fields produced a marked decay of the OCCA, but the red and green caused far more decay than the blue and orange fields. Further experiments showed that the blue and orange fields caused much the same degree of decay to white fields of the same luminance (Fig. 8.10b). These experiments suggest that the large decay caused by red and green homogeneous fields was not merely a result of chromatic stimulation, but was caused by specific wavelengths of light which were the same as those used to induce the McCollough effect.

8.4.2 Comparison of left/right oblique with horizontal/vertical achromatic gratings

In this experiment the oblique and the horizontal/vertical grating fields were the same size (12°x12° angular subtense at the eye) and the same average luminance. Both sets consisted of gratings which had the same spatial frequency as the test and induction gratings. The results (Fig 8.11a) show that the decay caused by the left and right oblique gratings (i.e. those of the same orientation as the induction gratings) was greater than that caused by the horizontal and vertical gratings, although both caused a marked decline of the OCCA. When the horizontal and vertical gratings were compared with white fields of the same average luminance, it was found that the gratings produced slightly greater decay (Fig. 8.11b). The difference in effectiveness between the stimuli was not as great as that between oblique gratings and white fields (see Fig. 8.9).

Fig. 8.11a. Comparison of oblique with horizontal/vertical gratings

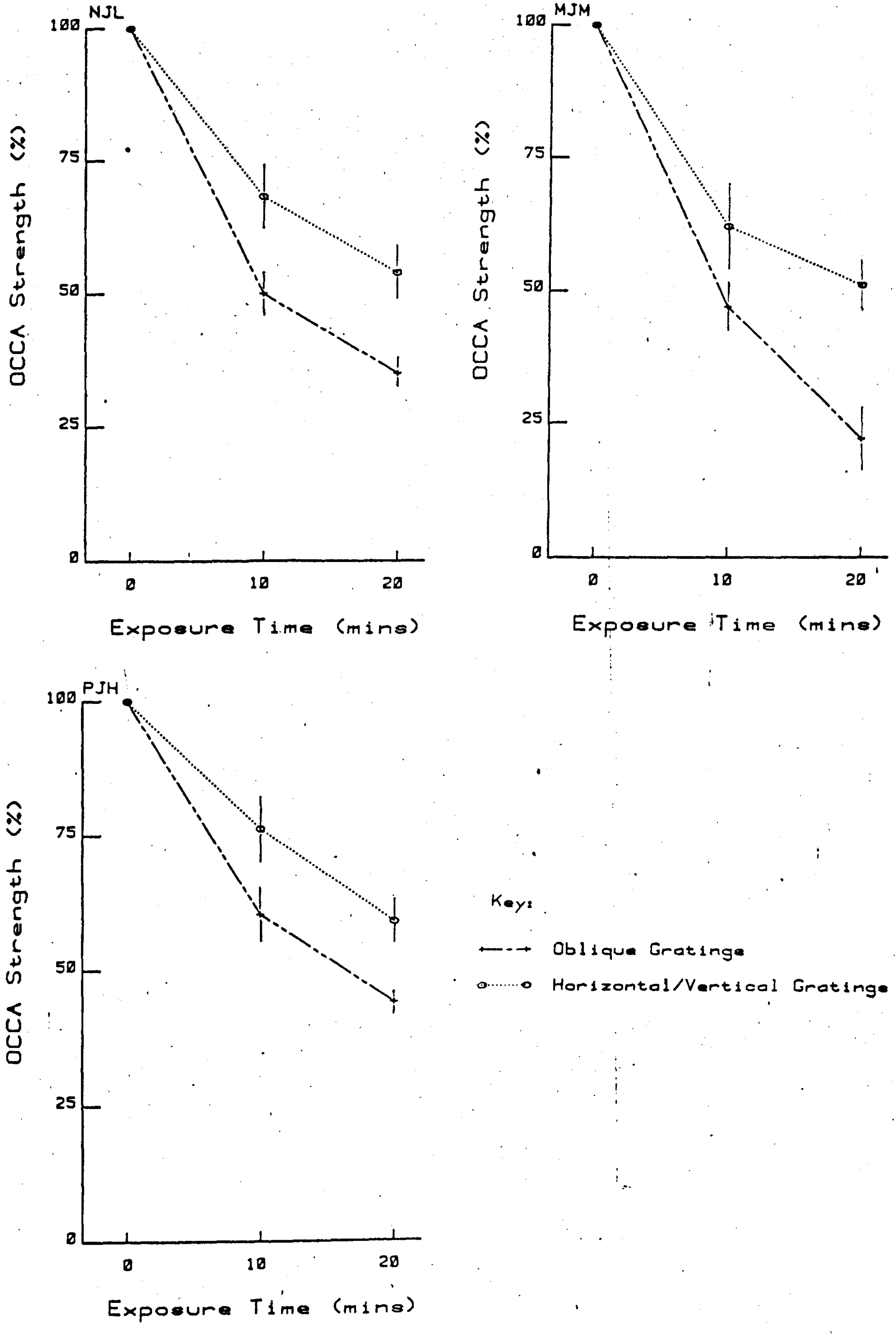
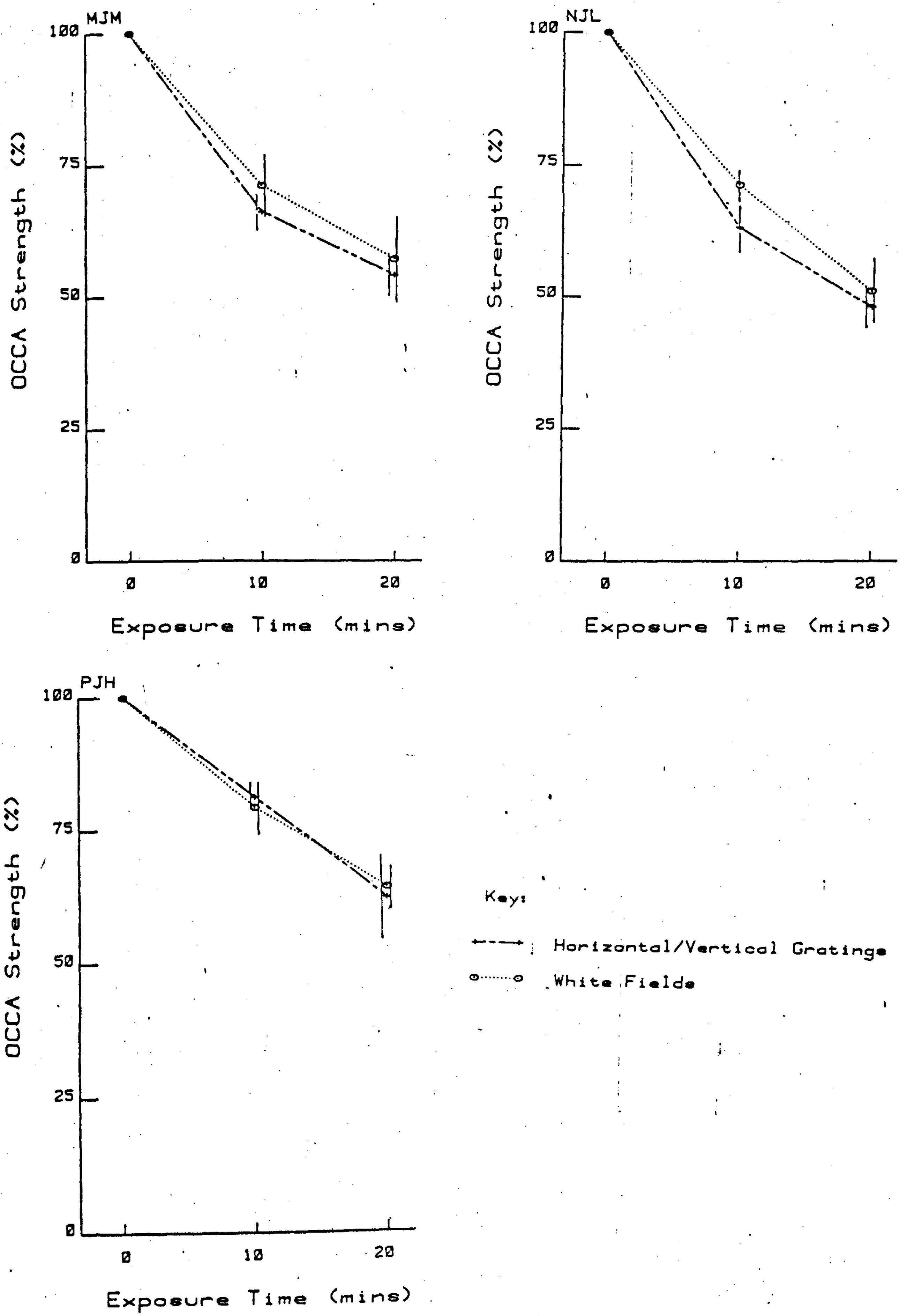


Fig. 8.11b. Comparison of horizontal/vertical gratings with white fields



8.5 Conclusions

The general conclusion from the experiments is that variation of visual stimuli presented after induction can produce large differences in the decay rate of the McCollough effect. The decay ranged from approximately 8% produced in (briefly interrupted) darkness to 80% produced with homogeneous red and green fields. Even small differences in stimuli caused a marked effect upon the decay rate (for example the difference between oblique and horizontal/vertical gratings). It is therefore entirely plausible that the variation in the decay rates reported in Chapter 4 were due to small changes in the conditions during decay. To take a mundane, but entirely possible example, if the experimenter or subject was wearing black or dark clothes on one occasion and bright red or green on a second occasion, one would expect a greater decay on the second. Some of the differences in the visual stimulation during decay were possible to control in future experiments (by wearing a standard white laboratory coat, for example) but others were not. The laboratory used for the experiments abounds in high contrast edges of varying orientations as did the the materials subjects handled in between decay measurements. The only possible way of obtaining standard stimulation during decay would be to ask subjects to gaze throughout at a large homogeneous field. This would not only be inhumane but would have drastically reduced the number of (unpaid) volunteers!

In addition to revealing sources of variability, these experiments have clarified some of the past data. In common with previous reports by MacKay and MacKay (1975a) and contary to those of Skowbo et. al. (1974) they have shown that darkness causes very little decay. Achromatic gratings of the same orientation and spatial frequency as the induction gratings produced a rapid decay as reported by Skowbo et.al. (1974) and Skowbo & Clynes (1977). Whereas Skowbo et.al. found that darkness, room illumination and homogeneous chromatic fields had the same effect upon decay, this study has indicated significant differences, the decay being largest when homochromatic fields were presented, and smallest in darkness. The differences in the results may have been due to variation in experimental method (see Section 8.2).

All past reported research about the effects of visual stimuli upon decay have used achromatic gratings and homogeneous chromatic fields which comprised the same component stimuli used to induce the McCollough effect. The experiments reported in this chapter have shown that less decay was produced by either gratings or coloured fields which were different from those used in the induction procedure. Unfortunately, there has only been time to study the effects of gratings at 45° (i.e. maximum) from the orientations used during induction, and of coloured fields of greatly different wavelengths from those used during induction. It would be informative to study the effects of small changes in wavelength and orientation and of changing the spatial frequency of the gratings upon the decay, since these experiments would be of theoretical interest. The results, however, have shown that it is not just chromatic or patterned stimuli which produce a fast decay of the McCollough effect, but chromatic or patterned stimuli which have the same charateristics as those used to induce the aftereffect. Following their results showing that the McCollough effect does not decay in darkness, MacKay & MacKay (1975b) postulated that the aftereffect was due to associative habituation of synaptic couplings. This view may be supported by the observation that the greatest decay is caused by components of the stimuli used to induce the OCCA; since the the recovery from adaptation may depend upon specific disruption of selective changes in the synaptic couplings.

CHAPTER 9 EFFECTS OF VISUAL STIMULI PRESENTED BEFORE INDUCTION

9.1 Introduction

One aspect of the experiments which was impossible to control fully was the visual stimulation to which the subjects were exposed prior to induction. Some of the variation observed in the initial strength after identical induction periods may have been due to differences in the stimulation before the experiments began.

Although stimulation prior to induction may be an important factor in the establishment of the McCollough effect, there has been little research reported in this area. It has been claimed, however, that gratings presented before induction 'interfere' with the McCollough effect and that high luminance gratings have more effect than low luminance gratings (Skowbo, 1979). A number of experiments were performed to investigate the effect of various stimuli presented before induction of the McCollough effect.

9.2 Monocular stimulation

The general experimental procedure (see Chapter 3) was varied slightly for all the experiments reported in this chapter. Subjects performed a pre-test measurement after 10mins. under standard illumination, as normal, but then they were subjected to a variety of visual stimuli for 20mins. Following this exposure the experiments proceeded as usual.

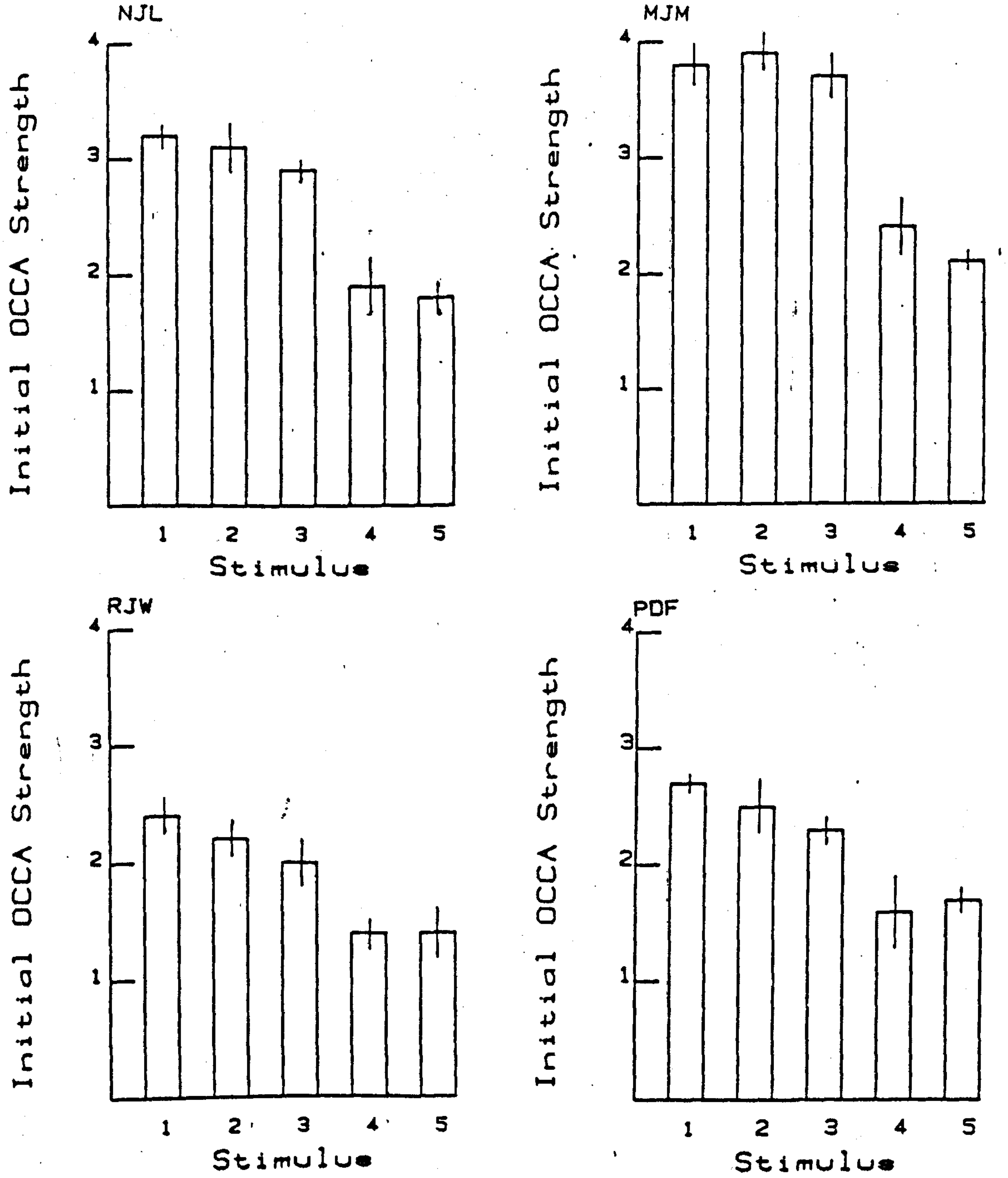
In these preliminary experiments McCollough effects were induced and tested monocularly after exposure to 5 types of visual stimuli:

1. Complete darkness
2. Room illumination
3. White fields
4. Alternating orthogonal achromatic gratings (of the same orientation and frequency as the induction stimuli)
5. Alternating red and green homogeneous fields

Stimuli 3,4 and 5 were presented at 5s intervals; 3 and 4 with no dark intervals; and 5 with a 1s dark interval. The averaged results of two runs for 4 subjects are shown in Fig 9.1, which reveals that both the red/green fields and the achromatic gratings presented before induction reduced the strength of the McCollough effect by approximately the same, large extent. Room illumination and darkness were associated with the smallest reduction and white fields with a slight reduction in McCollough effect strength.

It is of interest to compare the results with those of the experiments concerning the effect of varying visual stimulation after induction (Chapter 8). Homogeneous chromatic fields and achromatic gratings presented before induction result in a small aftereffect and if presented after induction cause a rapid decay. White fields and room illumination were associated with a relatively small decay if they were presented after induction and a large OCCA if shown before induction. It is interesting therefore that darkness prior to induction has the same effect as normal room illumination, since the results of Chapter 8 and of MacKay and

Fig. 9.1. Effects of various stimuli presented before induction.



Stimuli Conditions

1. Darkness
2. Room Illumination
3. White Fields
4. Achromatic Gratings
5. Homogeneous Chromatic Fields

MacKay (1977b) have shown that darkness after induction can reduce, or stop, the decay of the McCollough effect. Some experiments in Chapter 5 also indicate that long periods of darkness before induction have little or no effect upon the strength of the McCollough effect.

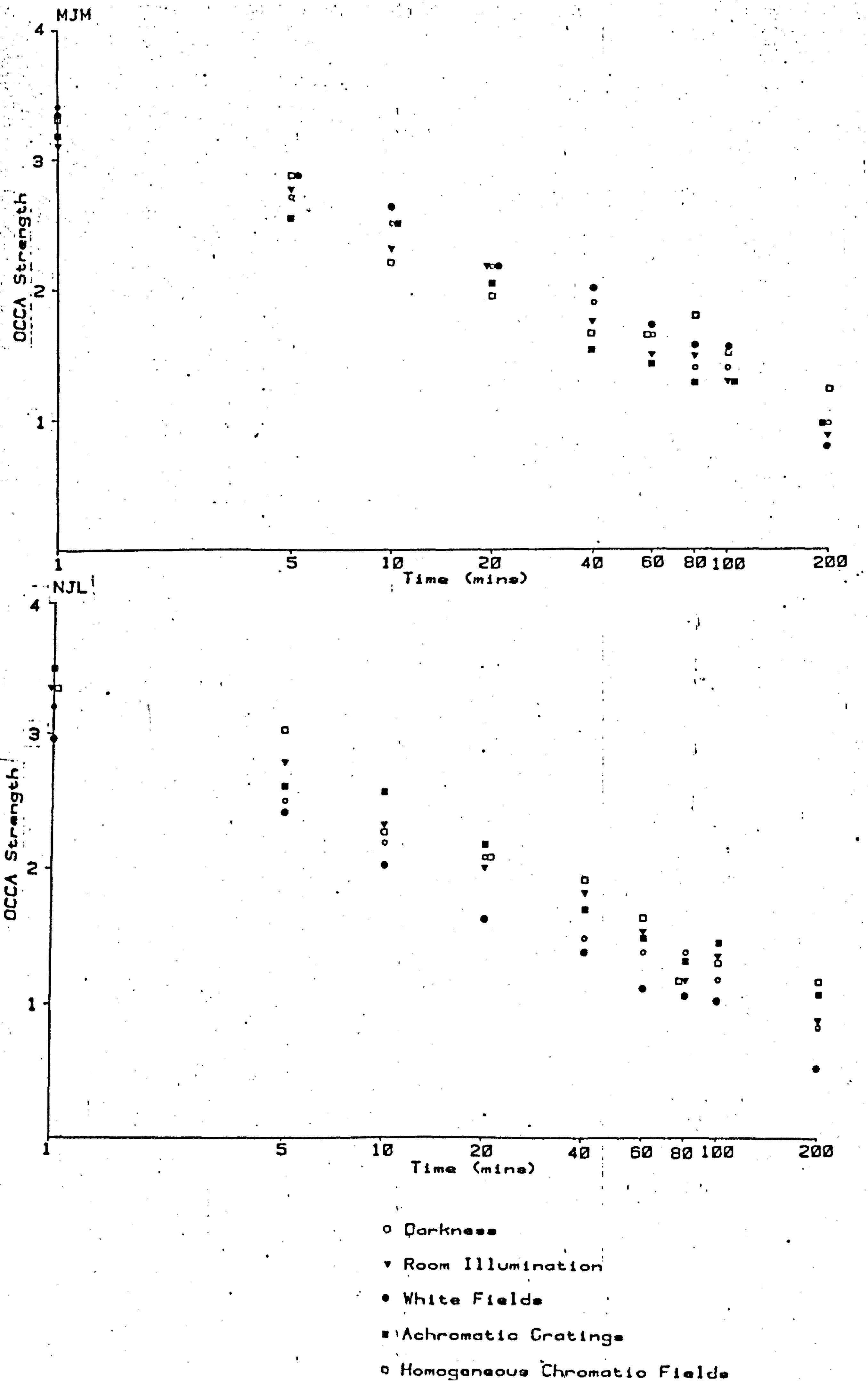
9.3 Effects of stimuli prior to induction upon decay

The results of Chapter 8 have shown that the stimuli used above had very different effects upon the decay rate of the McCollough effect when they were presented after induction. The experiments of Section 9.2 were therefore repeated, but the decay rates were measured to see whether the stimuli affected the decay rate when they were presented before induction. The results (Fig. 9.2) reveal that different stimuli presented before induction did not affect the decay rate of the OCCA although they had varying degrees of influence upon the initial strength.

9.4 Dichoptic comparisons of the effect of stimulation before induction

Though the results of Section 9.2 were consistent from run to run, preliminary experiments had revealed that the initial strength of the McCollough effect varied widely from day to day. Thus the hypothesis that the above results were due to normal variation, and not to the effects of the stimuli before induction, cannot be dismissed. Different stimuli were therefore investigated by comparing their effects, when presented to different eyes, upon a binocularly induced McCollough effect, since preliminary experiments

Fig. 9.2. Effects of visual stimulation before induction upon decay



had revealed that aftereffect strengths in each eye were similar following binocular induction. The tachistoscope was used to present the white, red and green fields and the gratings. These were presented for 5s with a 5s 'off' interval, each eye being stimulated during the 'off' interval of the other to avoid dichoptic interaction. The darkness condition was produced by a light-tight patch.

9.4.1 Comparison of homogeneous chromatic fields with darkness

A comparison of the effect of red and green fields and darkness presented before induction is shown in Fig 9.3, which indicates that in all 4 subjects the eye stimulated by the chromatic fields developed a much lower OCCA strength. This result is consistent with those of Section 9.2, but the direct comparison does not show whether the reduced aftereffect was caused by the difference in luminance or by the chromatic stimulation (see Section 9.4.3).

9.4.2 Comparison of achromatic gratings with darkness

The results of comparing the effects of achromatic gratings with darkness (Fig. 9.4) are again consistent with those of Section 9.2. They show that the aftereffect was much lower in strength in the eye which had been stimulated by achromatic gratings before induction. As in the previous experiment, the results do not reveal whether the reduction in aftereffect was caused by the difference in luminance to the eyes, or by the patterned stimuli (see Section 9.4.4).

Fig. 9.3. Comparison of Homogeneous Chromatic Fields with Darkness

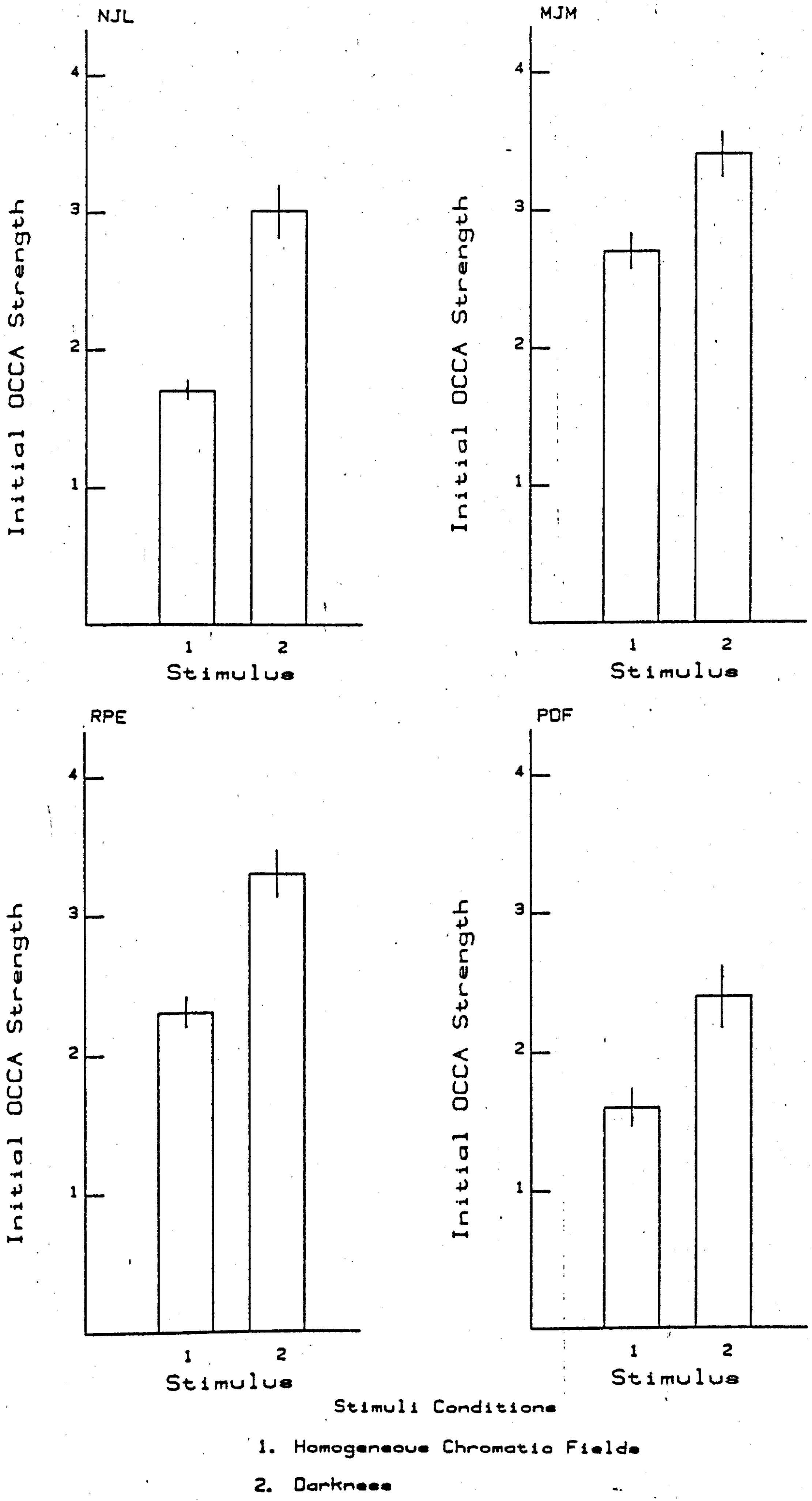
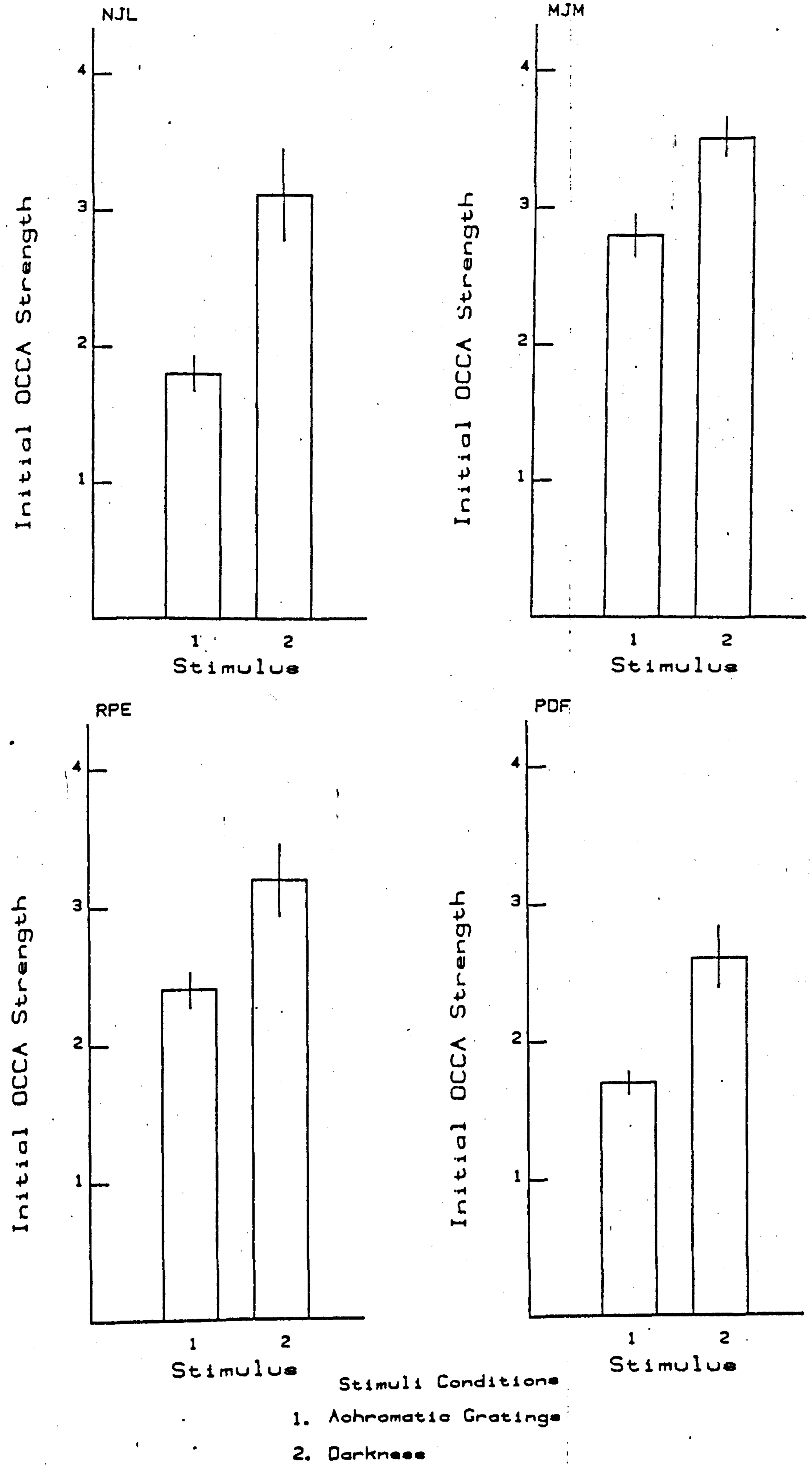


Fig. 9.4. Comparison of Achromatic Gratings with Darkness



9.4.3 Comparison of homogeneous chromatic fields with white fields

After prior stimulation with red and green fields the OCCA was substantially lower than in an eye which had been stimulated with white fields (Fig. 9.5). Previous experiments have revealed that red and green fields caused more reduction than darkness. This may have been caused by luminance difference, but since the white fields were of approximately the same luminance as the chromatic fields, it seems that the chromatic information caused the reduction.

9.4.4 Comparison of achromatic gratings with white fields

A comparison of the effects of prior exposure to achromatic gratings and to white fields (shown in Fig. 9.6) revealed that the white fields were associated with a much larger aftereffect. The strength of the McCollough effect in the eye stimulated by the white fields was similar, for each subject, to the strength found in the previous section when the same stimulation was used. Since the luminances were now approximately matched the results indicate that it was the patterned stimulation of the gratings that caused the observed reduction in OCCA strength.

9.4.5 Comparison of white fields with darkness

As a control experiment the effect of darkness upon the strength of a subsequent McCollough effect was compared with the effect of white fields. The results (Fig. 9.7) reveal that for all 4 subjects McCollough effects following darkness or white field stimulation were similar. It appears that differences in luminance

Fig. 9.5. Comparison of Homogeneous Chromatic Fields with White Fields

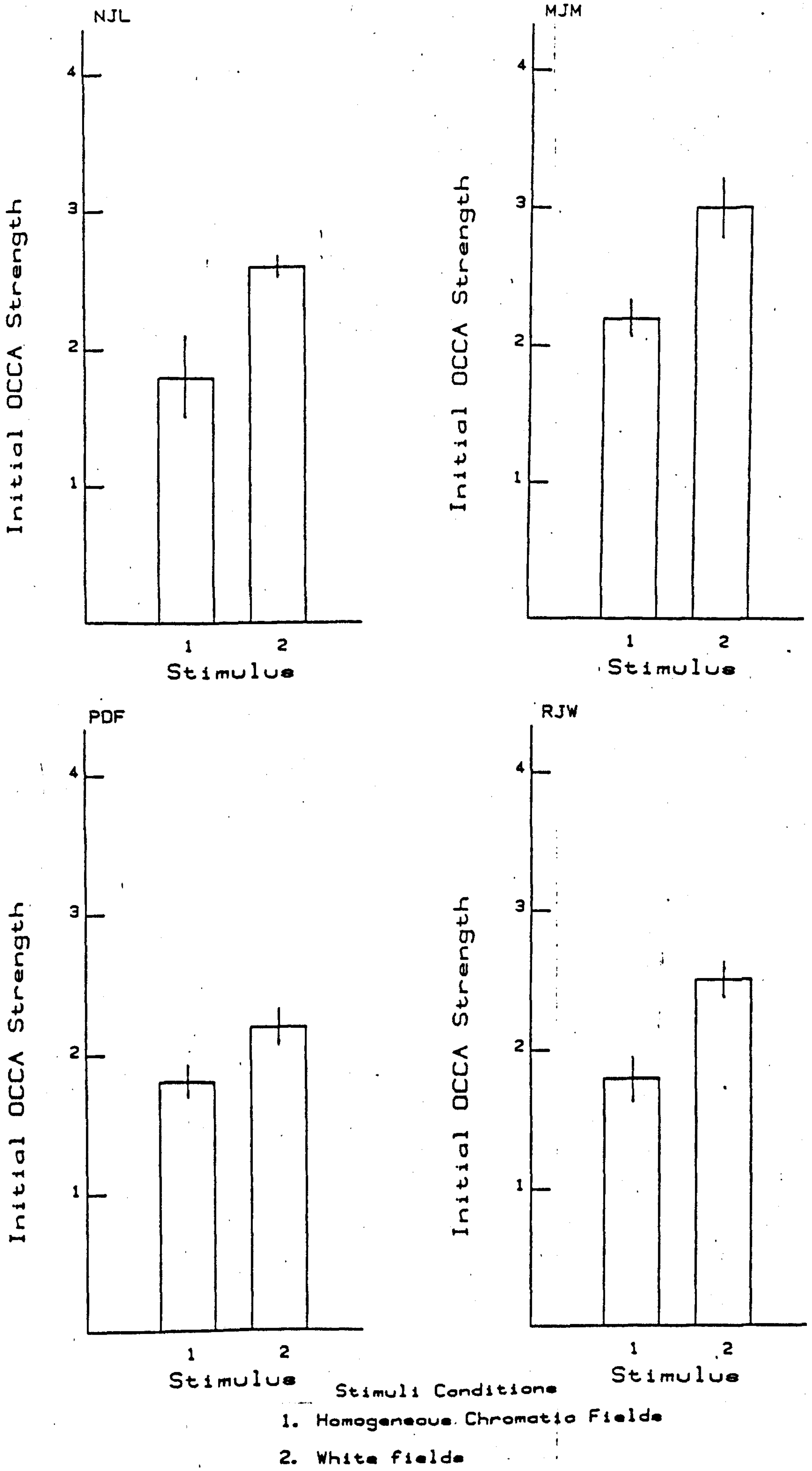


Fig. 9.6. Comparison of Achromatic Gratings with White Fields

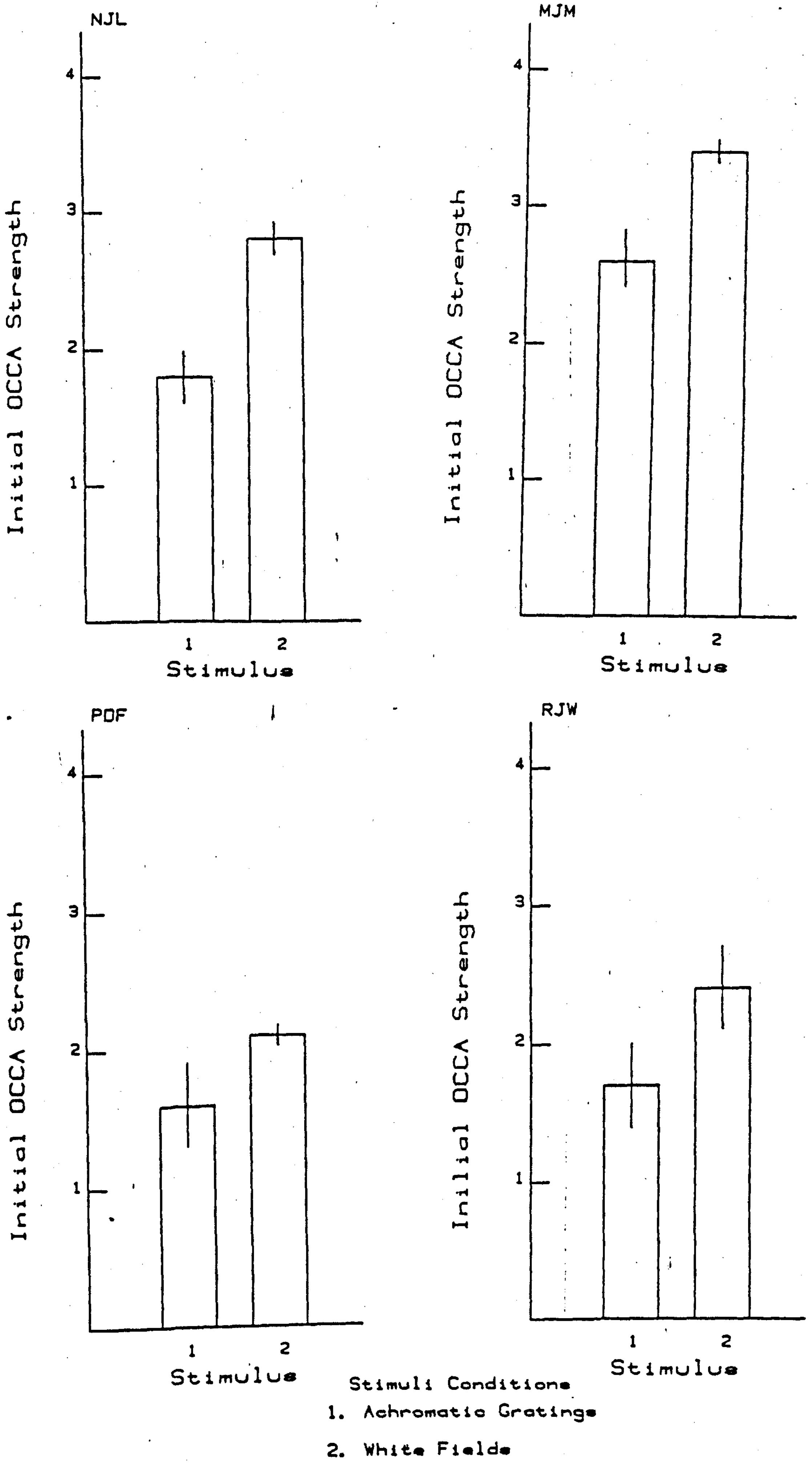
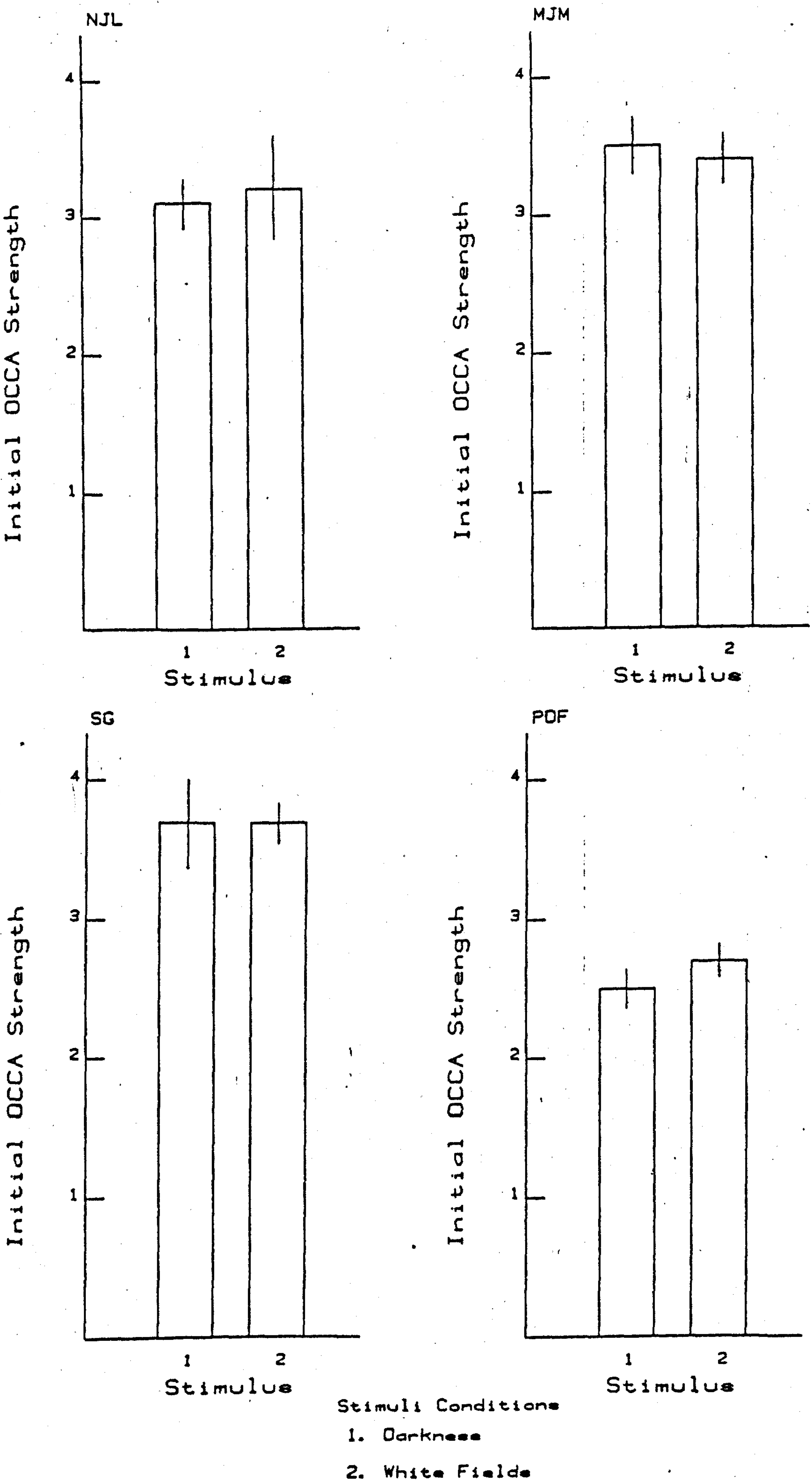


Fig. 9.7. Comparison of Darkness with White Fields



before the induction of the OCCA do not have a large effect upon the initial strength.

The similarity between the dark and white field conditions is interesting, since Skowbo (1979) has shown that differences in the luminance of gratings presented before induction do affect the strength of the McCollough effect. Since the results of Section 9.4.4. have shown that achromatic gratings reduce the aftereffect strength to a much larger extent than white fields of the same average luminance it is possible that the data presented by Skowbo (1979) were not merely the result of luminance differences per se, but were caused by luminance-dependence of the effectiveness of the grating stimulus.

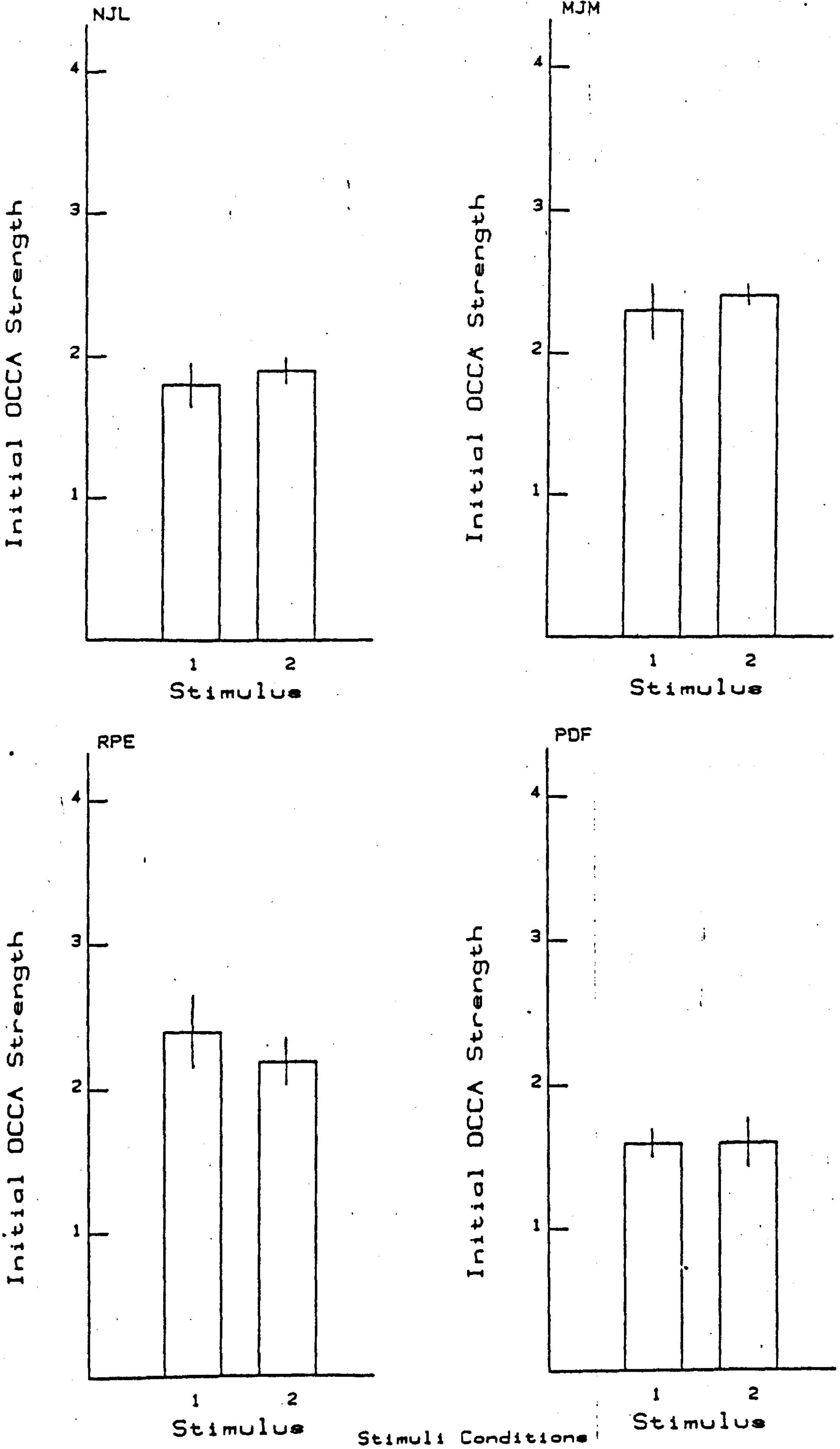
9.4.6 Comparison of achromatic gratings with homogeneous chromatic fields

Dichoptic interaction between the gratings and the coloured fields was avoided by presenting the stimuli to each eye during the 'off' interval of the other. The results (Fig. 9.8) show that the effects of both stimuli upon the initial strength of the aftereffect were approximately the same. For both conditions the OCCA was lower than the average aftereffect usually found for all subjects.

9.5. Effect of grating orientation

Following the results of Section 8.4.2, showing that horizontal and vertical gratings had less effect upon decay than oblique gratings (or gratings of the same orientation as those presented

Fig. 9.8. Comparison of Homogeneous Chromatic Fields with Achromatic Gratings



Stimuli Conditions

1. Homogeneous Chromatic Fields

2. Achromatic Gratings

during induction), the effect of grating orientation before induction was investigated. The experimental procedure was the same as that of Section 9.4. and the results (Fig. 9.9a) are averaged over 2 to 3 runs. During each of these runs, left and right oblique gratings were presented to one eye and horizontal and vertical gratings to the other. Fig. 9.9 shows that the initial strength of the aftereffect, following the presentation of the oblique gratings, was much lower than the initial strength after viewing alternating horizontal and vertical gratings (i.e. gratings of different orientation from those used during induction). Further experiments showed that the effect of horizontal and vertical gratings was not significantly different from that of white fields of the same average luminance (Fig. 9.9b).

After these experiments it was decided to investigate the effects of prior exposure to gratings of a number of different orientations to find whether the orientation had a progressively different effect. Gratings of 5 orientations were compared with the oblique gratings. These were: 10, 15, 20 and 30 and 45 degrees different in orientation from those used during induction (oblique). Since the aftereffects were of different strengths on each run, the effect of the gratings of varying orientations upon the initial strength of the aftereffect have been converted to a percentage of the strength in the eye which was presented with the oblique gratings. The results for 4 subjects are shown in Fig. 9.10. Point 0 from the adaptation stimuli represents runs in which oblique gratings were presented to both eyes and for clarity the results were put at 100%, since the strength in either eye was only a few percent different. The results to the left of this point represent

Fig. 9.9a. Comparison of Oblique with Horizontal/Vertical Achromatic Gratings

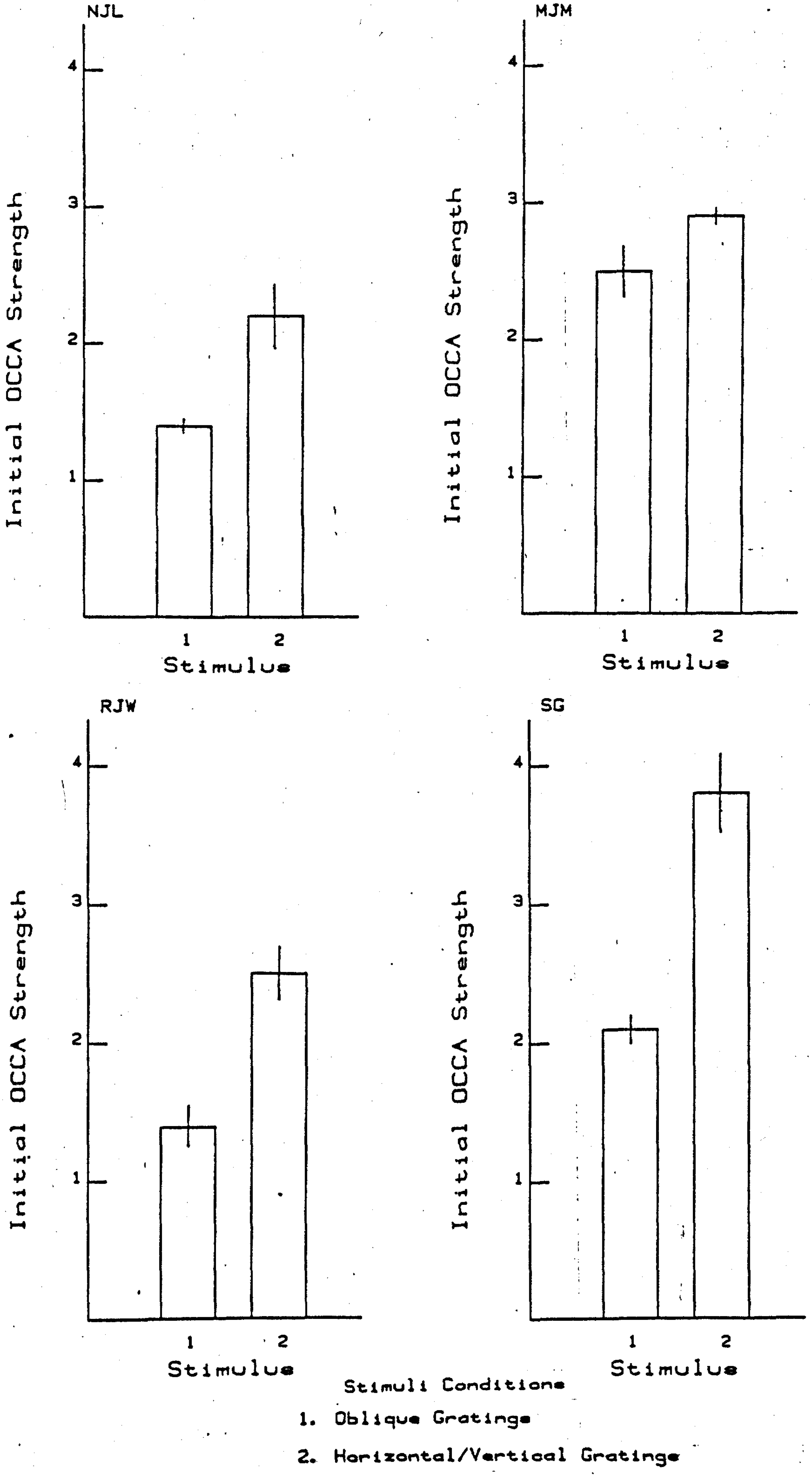
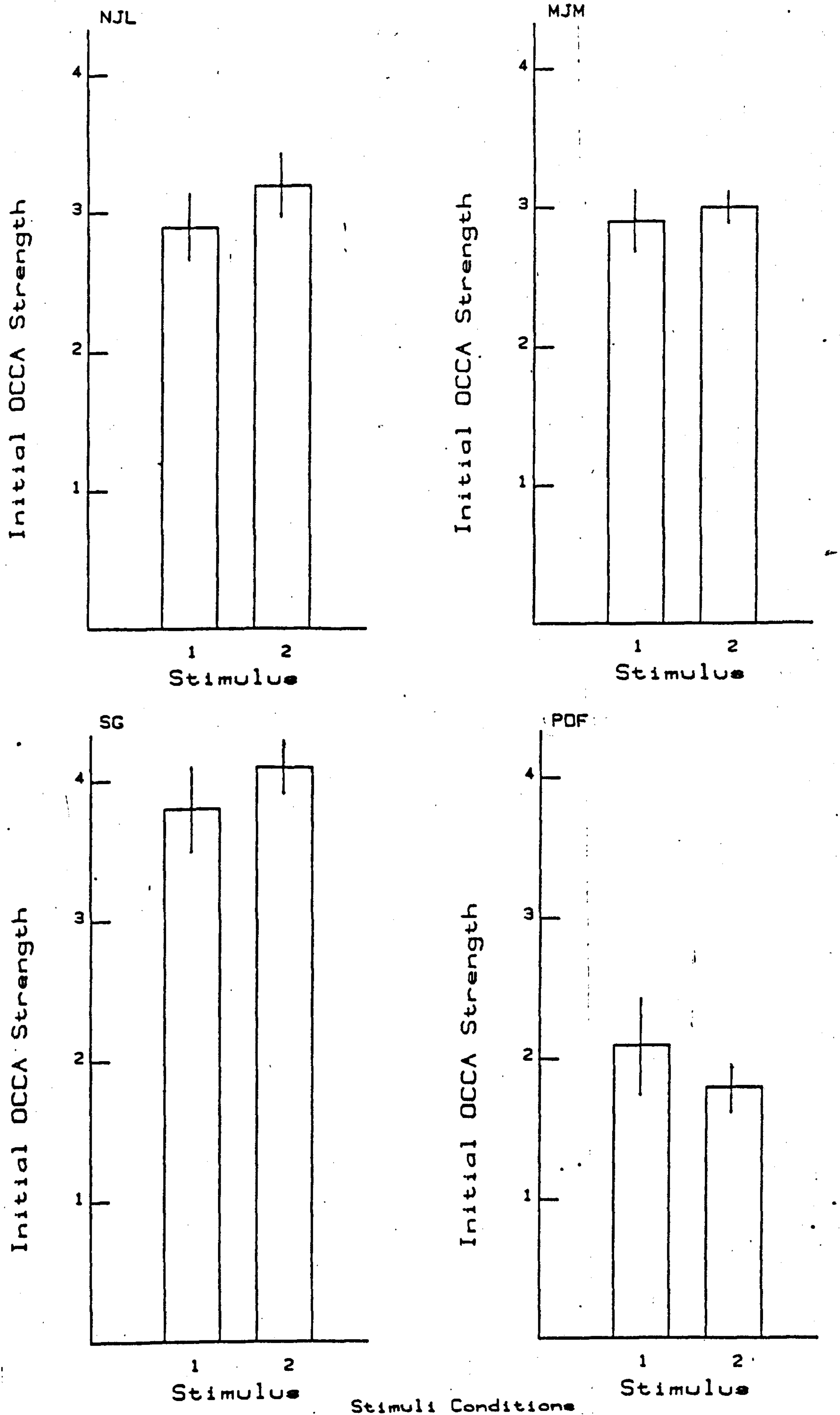


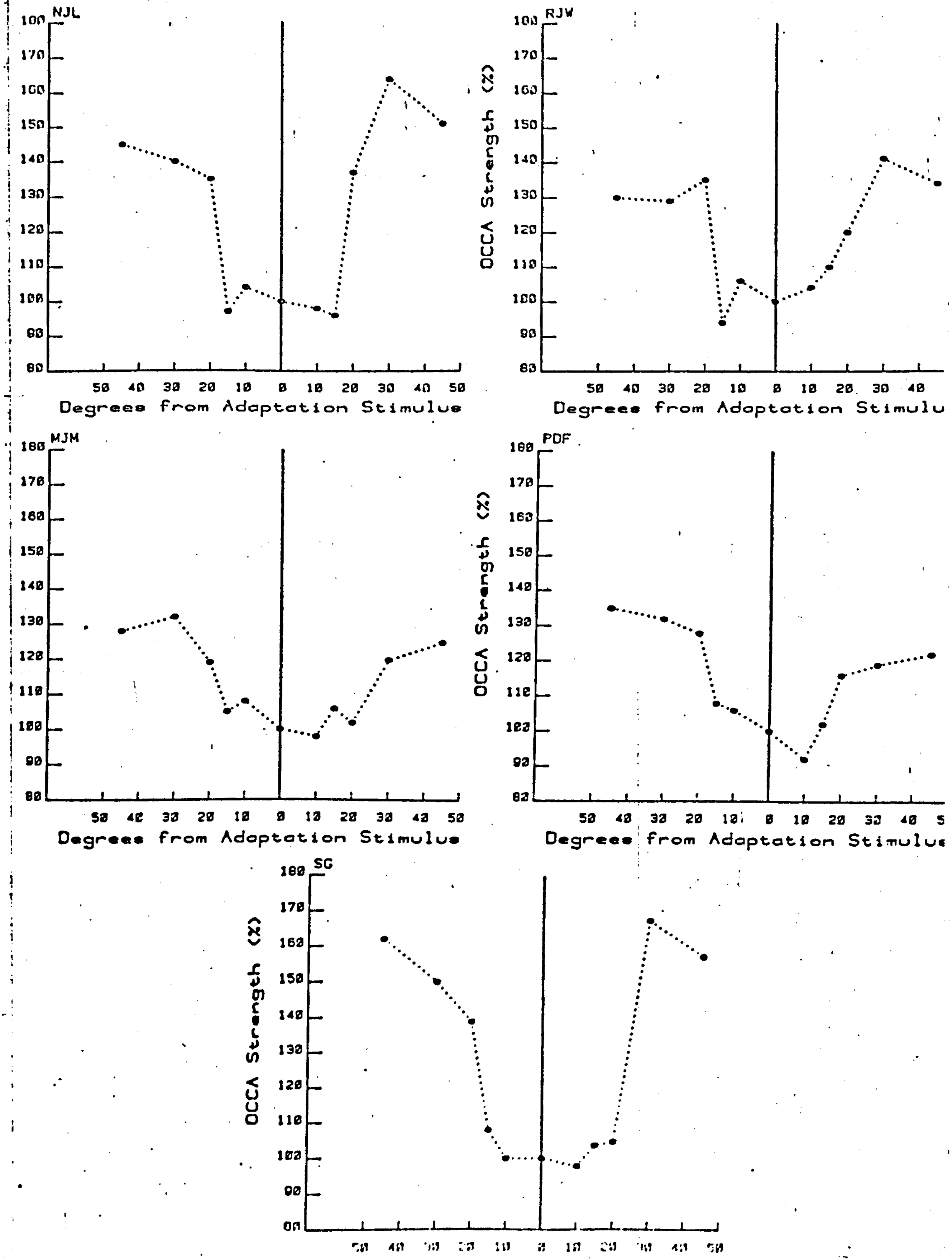
Fig. 9.9b. Comparison of Horizontal/Vertical Achromatic Gratings with White Fields



Stimuli Conditions

1. Horizontal/Vertical Gratings
2. White Fields

9.10. Effect of gratings of various orientations



runs in which the left eye was the 'standard' (i.e. the left eye was presented with oblique gratings) and the results to the right represent runs in which the right eye was the standard.

The graphs reveal that the OCCA strength resulting from inductions following the prior presentation of gratings was strongly dependent upon their orientation. However, the effect of varying the orientation was not graduated but had a specific 'cut off' point. Gratings of orientations 10 and 15 degrees from the oblique gratings had a similar effect to that of oblique gratings, sometimes producing slightly lower, and sometimes slightly higher, aftereffects. Gratings of orientations 30 and 45 degrees from the oblique, on the other hand, always produced much less reduction in OCCA strength than the oblique. The gratings which were 20 degrees from the adaptation stimuli had a variable effect upon the different subjects. In general, therefore, it seems as if the reduction in the McCollough effect caused by prior grating presentation occurs only if the grating orientations are within 15 to 20 degrees of those used to induce the aftereffect.

The figure of 15 degrees is interesting since Campbell & Maffei (1970), using evoked potential data, have demonstrated that selectivity to orientation in the human visual system was "so high that a channel was not influenced by another 15 degrees away".

9.6. Effect of different colours

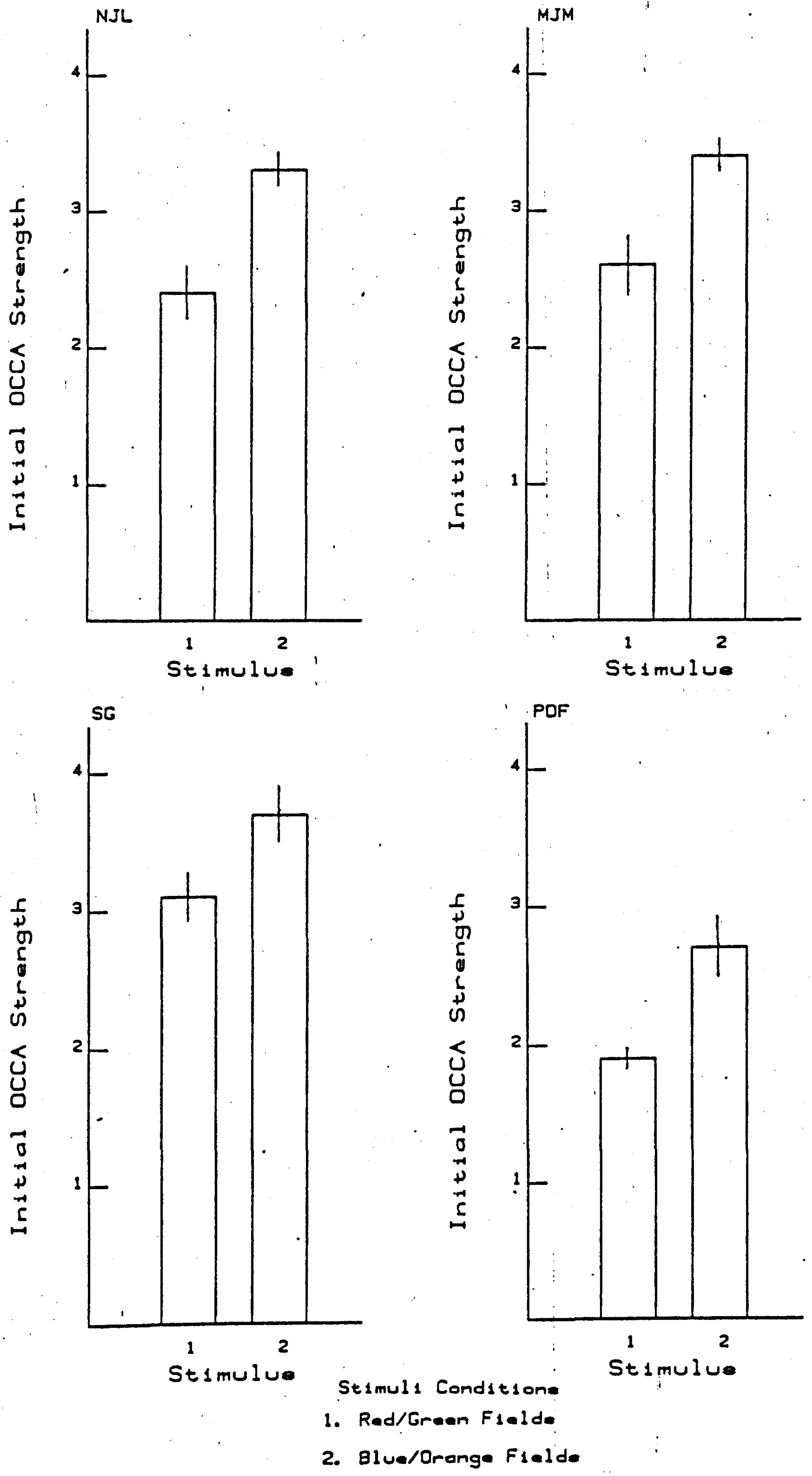
The experiments of the last chapter showed that the decay of the McCollough effect was greatly increased by the presentation of red and green homogeneous fields (the same colours that were used during induction) but that other colours had no more effect than white fields. Following the results of Section 9.4.6, which indicated that red and green fields presented prior to induction produce a large reduction in OCCA strength as compared to white fields, it was decided to investigate the effects of prior exposure of chromatic fields of different wavelengths.

The effects of red and green fields prior to induction were compared with blue and orange fields (Cinemoid 19 and Kodak 558-13 respectively). The results (Fig. 9.11) show that presentation of the red and green fields caused a much lower OCCA strength than the blue and orange. This experiment suggests that the reduction caused by the red and green fields was not merely a result of chromatic stimulation, but was a result of specific wavelengths of light.

9.7. Conclusions

The experiments of this chapter have shown that different visual stimulation, received before induction, can have a varied effect upon the initial strength of the McCollough effect. Some of the variation of the initial strength observed in the preliminary experiments may, therefore, have been due to differences in the visual stimulation before induction either before entering the laboratory or during the 10mins. in standard room illumination. One factor which may have caused variation was the pre-test measurement, since the test pattern consisted of achromatic gratings of the same orientation and spatial frequency as the induction gratings, and these have been shown to cause a large reduction in the initial

Fig. 9.11. Comparison of Red/Green with Blue/Orange Homogeneous Fields



strength of the McCollough effect. There were considerable differences in the time taken to perform the pre-test, particularly amongst the more naive subjects, and it now seems probable that these differences had significant effect upon the strength of the OCCA. One way of overcoming this problem would be to introduce a standard exposure of the pre-test gratings before each experiment.

Some of the results have indicated that gratings of orientations within 20 degrees of the inducing stimulus orientation, presented before induction, have the greatest suppressive effect upon the establishment of the McCollough effect. This fact, together with the results showing that chromatic fields of the same wavelength as those used during induction produce a small OCCA, may indicate some kind of habituation of the psychophysical 'channels' between which associative couplings are formed during induction.

CHAPTER 10 GENERAL CONCLUSIONS

The overall purpose of the research presented in this thesis was to identify some of the causes of inter and intrasubject variability the strength and the decay of the McCollough effect. A number of experiments have identified specific factors that can cause variability.

1. The initial strength of the McCollough effect is strongly influenced by prior sleep duration. (a) Reduction of sleep duration by about one third of normal caused a large drop in aftereffect strength; but (b) further reductions had no effect. (c) Increases above the normal sleep duration resulted in a larger aftereffect. Changes in an individual's sleep duration by a few hours can thus result in large intrasubject variation; and differences in sleep habits can result in significant intersubject variation of the strength of OCCA induced under standard conditions. Decay slopes (on log-log plots), however, were not affected (Chapter 5).
2. Both the initial strength and the decay of the McCollough effect are affected by the time of day and seem to follow a diurnal rhythm. In line with past research (MacKay, 1978), the rate of decay was found to decrease during the late evening - early morning. The initial strength also drops during this period. The exact timing of these diurnal changes varies with the phase of the sleep rhythm of the subjects (Chapter 6). Variability of both strength and decay of the McCollough effect may therefore occur as a result of performing experiments at late hours of the day or of subjects shifting the timing of their sleep.
3. The effects of sleep and time of day upon the strength of the

OCCA seem to have a common basis. Small aftereffects produced after sleep deprivation do not undergo the normal diurnal reduction but occur later in the evening. In addition, the high and low aftereffect levels found with variation in sleep and time of day are approximately the same for each subject. Inter and intrasubject variability can be reduced only by controlling both the sleep duration and the timing of the experiments for all subjects.

4. The decay of the McCollough effect is strongly dependent upon the type of visual stimulation received after the induction process. In line with past evidence, it was found that (briefly interrupted) darkness causes very little decay (MacKay and MacKay, 1974a, 1975a, 1977b) and that achromatic gratings of the same orientation as the induction gratings, cause a rapid decay (Skowbo et.al., 1974; Skowbo, 1979). Generally, however, the most rapid decay was found to be caused by homogeneous chromatic fields of identical wavelengths to those used during induction. Other visual stimuli, including white fields and achromatic gratings or chromatic fields, different from those used during induction, cause greater decay than darkness but less decay than stimuli of similar characteristics to the induction stimuli (Chapter 8). The large variation caused by different visual stimuli may be responsible for some of the variability of the decay of the OCCA. This variability can only be controlled by a strict experimental procedure.

5. Variation of the visual stimulation prior to induction causes significant differences in the initial strength of the McCollough effect. Stimulation by oblique gratings or red and green fields (i.e. stimuli with identical characteristics to the induction stimuli) caused a marked reduction in the OCCA strength as compared with other types of stimulation (including: white fields, darkness,

blue and orange fields and horizontal and vertical fields). The reduction of the aftereffect by gratings was limited to those of orientations within 15- 20 degrees of the induction stimulus orientation. Visual stimulation prior to induction was found to have no effect upon subsequent decay (Chapter 9). Differences in visual stimulation before induction can, therefore, introduce variability of the initial strength. One particularly relevant source of variability is the duration of exposure to pre-test patterns which consist of gratings of the same orientation as the inducing patterns.

6. Amblyopic and stereoblind subjects exhibit different monocular, binocular, dichoptic and transferred McCollough effect results from normal observers. After binocular stimulation, the strength in amblyopic, or non-dominant, eyes is much lower than in the normal, or dominant, eyes. If the amblyopic eye is stimulated monocularly, the aftereffect strength is much larger. Normal subjects develop similar aftereffect strengths in both eyes after binocular stimulation and the strength is approximately the same after monocular stimulation. Amblyopic and some stereoblind subjects show large transfer (up to 50%) of the McCollough effect, but only from the amblyopic eye. It is generally agreed that normal observers do not show substantial transfer (less than 10%). Finally, normal subjects develop similar 'anomalous' McCollough effects when gratings are presented to either eye. However, when the gratings were presented to amblyopic eyes or non-dominant eyes, both the 'anomalous' and the McCollough effects were larger than when the gratings were presented to the normal eye (Chapter 7). These differences between normal observers and those with visual abnormalities could lead to intrasubject variability, especially in

studies of dichoptic or transferred McCollough effects.

Pressure of time has prevented extensive exploration of a number of topics and many experiments have suggested a need for further research. One general point to emerge from all the experimental chapters was that there was a need to compare the effects of various factors upon the McCollough effect with other colour contingent aftereffects since a number of investigators (for example, Skowbo, Gentry, Timney and Morant, 1975) have suggested that these aftereffects are related. This is particularly true of the experiments reported in Chapter 7, since these have shown that the McCollough effect transferred more with amblyopic subjects than with normal subjects. Past research has showed that amblyopia reduces the transfer of a variety of achromatic aftereffects. It would be informative to investigate the effects of amblyopia upon the transfer of other colour contingent aftereffects, in order to find out if the McCollough effect is unique, or whether colour contingent aftereffects form a group, since research so far has indicated that all aftereffects contingent upon colour (including the McCollough effect) do not transfer in normal subjects. The experiments reported in Chapter 8 and 9, on the effects of various visual stimulation before and after induction, have helped reinforce the theory that the McCollough effect is an associative process. It would be informative to repeat these experiments, especially with stimuli which have similar characteristics to the induction stimuli, on other contingent aftereffects, in order to find out whether all such aftereffects are caused by associative processes.

Apart from this general point a number of the areas studied have suggested particular topics which are in need of further research.

1. The cause of the effect of sleep upon the McCollough effect must remain speculative until controlled EEG studies, measuring the type and duration of sleep, can be done. Also, since brain activity, particularly neurotransmitter production, is known to change rapidly during sleep and sleep deprivation, it would be of interest to artificially alter the levels of a variety of agents in order to investigate their effects upon the OCCA. Another source of information may be found in the study of the effects of sleep inducing or reducing drugs on the strength of the OCCA, particularly since a number of such drugs are known to alter the overall types of sleep.

2. A few experiments indicated that the influence of sleep loss upon the McCollough effect is cumulative. Though an arduous task, it may be productive to undertake a controlled investigation of the effect of repeated sleep loss. Such a project might also include a study of long-term diurnal effects, particularly that of changing diurnal rhythms (with, for instance, shift workers).

3. The difference in various McCollough characteristics, between normal and amblyopic or stereoblind subjects suggests that the effects of various other visual abnormalities, particularly those thought to be neural in origin, should be studied. Amblyopia was regarded as one particular defect in Chapter 7, but is known to be caused by several different factors, each producing a condition with its own characteristics. The effect of those different types of amblyopia, together with various colour deficiencies, could be studied.

4. Although the effects of visual stimulation upon the decay of the McCollough effect have been studied before, the experiments reported in Chapter 8 suggest a need for a number of more controlled investigations. In particular, it would be of interest to study the effect of gratings of various orientations and spatial frequencies and the effect of a number of colours of varying wavelength.

5. The experiments concerning the effect of visual stimulation presented before induction suggested that further studies in this area could produce some worthwhile results. Such studies could include the effect of varying the spatial frequency of gratings and of the effect of various colours.

6. Diet and drug intake have been recorded and controlled (as far as possible) in all the experiments reported in this thesis since a number of reports have indicated that some drugs, including caffeine and nicotine, affect both the strength and the decay of the McCollough effect (Shute, 1979; Amure, 1978, 1979). In order to fully control variability of the OCCA, it may be necessary to investigate the effects of all parts of the diet or at least those substances known to affect body metabolism.

7. The decay graphs throughout this thesis have shown that a large proportion of the decays were arrested between either the 5 and 10, or the 10 and 20 minute measurement. The decay rate before and after these periods was normal. This suggests that the OCCA decays readily at first but then undergoes a short period of stabilization. Further research is needed to examine this phenomena more closely.

Despite the varied nature of the subject matter, several broad conclusions have emerged from this thesis. Every experimental chapter has shown a need to identify and control those factors which have an influence upon the McCollough effect. One way of identifying factors causing variability is to note and record all details, even apparently irrelevant ones, about the subject and environment before, as well as during, each experiment. I am grateful to Dr. V. MacKay who suggested such a procedure when I started this research. I am reminded of a decay record which she showed to me on one portion of which was written "sitting on the step in bright sunlight preparing sprouts". Such attention to detail, kept on a permanent record, creates a source of cross reference from which further experiments can isolate factors relevant to the McCollough effect.

Each chapter has, to a greater or lesser extent, indicated that the McCollough effect is caused by an associative process. The stark contrast between the effect of sleep and time of day upon the McCollough effect and their influence upon other visual tasks (acuity, simple aftereffects, etc.); and the similarity between the pattern of results of Chapter 5 and 6 to the reports concerning the effects of sleep and time of day upon memory and learning offers, at least circumstantial, evidence that the underlying processes causing the OCCA are associative. On the basis of their research showing that darkness stopped the decay of the OCCA, MacKay and MacKay (1975b) suggested that the McCollough effect was due to associative habituation of synaptic couplings. Two lines of evidence supporting this view were presented in Chapters 8 and 9. Several sets of data showed that where stimuli with characteristics identical to those of the inducing patterns (i.e. oblique gratings or red and green homogeneous fields) were presented after the induction, they caused a much greater decay of the McCollough effect than any other visual stimulation. Furthermore, when oblique gratings or red and green fields were presented before induction, the initial strength of the aftereffect was greatly reduced (but subsequent decay slopes were not affected). It is possible that when these stimuli are presented after induction, they disrupt specific synaptic couplings and thus reduce the strength of the OCCA. When they are presented before induction, they may cause habituation of the particular 'channels' between which associative couplings are formed during induction.

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APPENDIX A. METHODS OF MEASUREMENT.

A large proportion of the variability and conflict which exists in the McCollough literature may arise from the variety of methods used to measure the effect. Methods used have varied from simple verbal reports to some which have used equipment designed to match or cancel the effect. Some of these methods are examined below.

All methods used to indicate the strength of the McCollough effect yield only indirect measurements since the aftereffect itself is a property of the nervous system. Colour reports, or measurements, are not measures of the aftereffects but are evidence that the aftereffects are present. Methods of measurement are therefore subject to a number of desiderata. Firstly, they may depend on some factors which are incidental to the aftereffect. For example, the measurement may be affected if the luminance varies as the colour changes. Secondly, units of measurement should be expressed so as to yield useful estimates of the aftereffect strengths. Obviously as the aftereffect becomes more vivid, measurement scores would be expected to increase. However, one cannot be certain whether each increase of any measure represents the same increase in the aftereffect.

A.1. Verbal Reports.

A number of investigators have used verbal reports of the test pattern to determine the presence or absence of the McCollough effect (McCollough, 1965; Over and Lovegrove, 1973; White and Riggs, 1974; Wyatt, 1974; Vidyasagar, 1973; Schmidt and Finke, 1979). McCollough (1965) used verbal reports to test whether orientation colour contingent aftereffects could be induced. She found that only some of the subjects reported the effects possibly because they were typically quite desaturated. Verbal reports were used by Lovegrove and Over (1973) to determine whether the effect could be induced dichoptically. Unlike MacKay and MacKay (1973a, 1975a),who used a match and null technique, they found no evidence of dichoptic induction. The aftereffects induced dichoptically are smaller than those induced normally. The lack of any positive report may have been due to the very desaturated hues of the aftereffect which were only detected using a sensitive method of measurement.

Verbal reports are only useful to determine the number of subjects who detect an aftereffect. They do not give an indication of its strength. The decay of the effect, or the different strengths induced by various methods, cannot be investigated. Magnitude estimations have been used in attempts to give numerical strengths to the aftereffect (Stromeyer, 1969; Sharpe and Tees, 1978; Uhlarik and Osgood, 1974) but the small range of magnitude over which the McCollough effect exists makes this technique difficult. In addition, a subject's criteria for such an estimate may vary from test to test.

A.2. Short-term memory matching.

Some experiments have involved the use of coloured paper, or chips, to match the aftereffect (Stromeyer, 1972a; Foreit and Ambler, 1978; Ambler and Foreit, 1979). This method requires the subject to view a test pattern and then to choose the paper, or chip, which most resembles the hue seen. Such a method, however, relies on short-term memory matching. Newhall, Burnham, and Clarke

(1957) have shown that such colour matches are appreciably brighter and more saturated than matches using the normal method of simultaneous presentation. Short-term memory matching cannot, therefore, be regarded as an accurate representation of the aftereffect.

A.3. Orientation Change.

The McCollough effect is strongly dependent upon the relationship between the orientation of the test and induction gratings (Fidell, 1970; MacKay and MacKay, 1977a). Teft and Clarke (1968) have used this dependence to investigate the effect of changing the spatial frequencies of both the test and induction gratings. The degree to which test gratings of different spatial frequencies could be rotated before the aftereffect completely faded, was taken as a measure of the McCollough effect. Although this measure gives an indication of the strength of the effect the variable being measured is the range of orientations over which the effect remains visible.

A.4. Colour Matching

The hues seen on test patterns have been matched using projection colorimeters (Hirsch and Murch, 1972; Skowbo et al, 1974; Murch, 1971). Using such instruments the aftereffect can be expressed in terms of C.I.E. chromaticity coordinates. This method allows one to examine the decay and varying strengths of the effect. Murch (1971) and Hirsch and Murch (1972) have used a small adjustable central grey area to match the hue of the surrounding test pattern. Skowbo et al. (1974) have matched the aftereffect by presenting the test pattern to the left eye and a homogeneous adjustable field to the right eye. This method introduces the problem of binocular rivalry. All matching methods involve comparing gratings with a blank field which makes it difficult to match the luminances. The luminance of the blank field could be matched with either the luminance of the white lines or the average luminance of the test pattern. If it is matched with the average luminance the luminances of the white lines and the blank field will be different and this may affect the colour matching during the test. If it is matched with the white lines the average luminance of the two fields will be different. In addition, as the test pattern is viewed for some time, Mach bands may be produced due to the sharp luminance gradients (Davidson, 1966). The perceived luminance of the white lines will not be uniform and this further complicates any luminance match. Most investigators who have used the colour match method, have not specified the relationship of the test grating and blank field luminances (for example Skowbo and Clynes, 1977; Hirsch and Murch, 1972).

A.5. Null Methods.

The null method of measurement requires the subject to adjust the colour of the test pattern, until it appears achromatic. Fidell (1970) and Holding and Jones (1970) have used this method and have asked the subject to view each half of the test pattern separately. This procedure introduces two problems, firstly there is lack of a definite end point and secondly the subjects criteria for making the judgement may change between measurements. Riggs et al. (1974) and White (1976) have eliminated these problems by using two polarized filters which nulled the two halves of the test field simultaneously. The subjects were instructed to null the aftereffect until both halves of the test pattern were matched. This method provided a definite end point so that the strength of the McCollough effect could then be expressed accurately in terms of colorimetric purity.

Riggs et al. (1974) recognised a number of constraints of their method, some of which were only partially resolved. Firstly, the colours used to test the aftereffect must be exactly complementary to the aftereffect hues. However, they report that some strong effects could not be matched by any position of the filters. Secondly, the green and red components must be balanced for a null match to be made. This was only approximately achieved, since subjects varied so that some could not find a balanced position. Thirdly, the filament image should be homogeneous in the plane of the filters. Since this was not achieved, slight differences in luminance occurred on the test pattern. The fourth constraint mentioned by Riggs et al. was that the apparatus should be able to measure the strongest aftereffects. This applies to all methods of measurement. Riggs et al. reported that the longest exposures produced aftereffects which could not be measured without modification of the apparatus.

A.6. Match Interference.

The method of matching the McCollough effect by using interference produced by transparent birefringent tape, has been used by Shute (1976) and Amure (1979). This method matches the red hue of the aftereffect with the red light produced by removing green light. Two projectors were used, one projecting a test pattern and the second a blank slide. Two pieces of polaroid, with their axes of transmission parallel, and a rotating insert were arranged over the lens of the second projector. A transparent birefringent 1.5λ plate for green light (λ =535nm), with a retardation of 800nm, was placed in the rotating insert. As this plate was rotated between the parallel polars, a red interference colour was produced. The intensity of colour increased from zero to maximum as the angle between the slow direction of the wave plate and the transmission axis of the polars increased from 0° to 45°. The strength of the aftereffect was recorded as the percentage extinction of green light required to produce the red colour match. After a rotation of c° this was taken to equal $100\sin^2 2c$. However, due to the arrangement of the polarised filters the luminance of the match area changes as the colour varies. The change in the saturation of the colour was therefore confounded with a change in the luminance. Shute (1979) has reported that the matching was not impaired by the reduced luminance of the interference system. He estimated photometrically that the luminance was reduced by about 43%. It has been shown that low luminance test patterns produce stronger aftereffects than test patterns of high luminance (White, 1976). Although the test patterns remain at the same luminance, using this method, the area to which they are matched changes dramatically. Most investigators have removed or added the pre-induction to the post-induction measurements. Shute (1979) reports that he did not do this for two reasons: firstly, he believes that subthreshold McCollough effects, which are too small to measure, may be present; secondly, he concludes that the decay of the effect depends on the initial strength, no matter how this strength is achieved. However, Bradshaw (1978) reports that the effect is strongly dependent upon the induction 'on' and 'off' timing and that initial strength has little, if any, effect on decay.

A.7. Match and Null.

The methods of matching and nulling the McCollough efect can be combined to give a simultaneous match and null measure (MacKay and MacKay, 1973b; MacKay, 1978; Bradshaw, 1978). This method involves the use of a test pattern of two halves which have orthogonal gratings. Each half contains translucent windows which have gratings orthogonal to the surround. Filters behind the windows can be adjusted to match them to the hue of the surrounding gratings. At the same time the hue on the gratings of the windows are nulled. A detailed description of the method and apparatus used can be found in Chapter 3.

The match and null method gives a larger measure than either matching or nulling alone and can therefore be used to show small differences in the strengths of the aftereffect. This is an important consideration when studying the changes produced under different induction conditions or the gradual decline of the effect during decay. The method also provides a definite end point. However, there are a number of constraints. The apparatus should have been able to measure aftereffects of all strengths. Some very strong aftereffects could not be measured without changing the amount of white light which desaturated the colour of the filters. Secondly, the method used both a match and a null component and it should have been possible to match all aftereffect hues. Some subjects occasionally had difficulty in matching the green hue with the green colour produced by the filters. Thirdly, the matches were always performed in a slightly yellow light. This was added to the test surround to match the yellow produced by the red-green mix. The various tests and calibrations of the method are reported in Chapter 3.