THE MCCOLLOUGH EFFECT:
A STUDY OF SOME TEMPORAL CHARACTERISTICS

by

K. BRADSHAW

Dissertation presented to the University of Keele for the degree of Doctor of Philosophy.

May, 1978

Research Department of
Communication and Neuroscience,
University of Keele.

ABSTRACT

ACKNOWLEDGEMENTS

LIST OF CONTENTS

Page

ABSTRACT

A parametric study was made of the influence of the temporal parameters of stimulation on initial strength and rate of decay of the McCollough Effect.

Using a tachistoscope to accurately control stimulus presentation timings, it was shown that the length of both the period of stimulation and intervening dark interval can affect initial strength of the aftereffect, and decay slope on log-log plot. An interpolated period of diffuse achromatic illumination may impede establishment of the aftereffect, provided the period is sufficiently long and strategically timed. The evidence indicates that strength builds up most rapidly with lengthening of the stimulation period to a second or two. For these short stimulation periods, decay is reasonably well described by a straight line on linear-log plot. Periods longer than about three or four seconds induce aftereffects having a decay better described by a straight line on log-log plot. The mechanism involved may also be sensitive to the proportion of time given to coloured pattern stimulation.

Initial strength increases with lengthening of the duration of exposure, build-up being reasonably well described by a straight line on log-log plot. Decay slope on such a plot changes systematically for extremely long or extremely short exposures.

Temporal parameters of stimulation were also shown to affect dichoptic induction of McCollough-type aftereffects. Asynchronous onset or offset of stimulation in the two eye fields may impede, or prevent establishment of the aftereffect, timing differences of about two or three seconds being critical.

Further brief studies investigated interactions between eye channels

during monocular induction of the aftereffect, and the influence of various drugs on establishment and decay of the normal McCollough Effect.

ACKNOWLEDGEMENTS

The research reported here was carried out in the Research Department of Communication and Neuroscience. I am grateful to the Department for the use of equipment, and for free access to the available facilities.

It is also a pleasure to acknowledge the specialist help so generously given by many members of the Department. Professor D.M. MacKay suggested the project and supervised the research. I am especially grateful to him for his guidance, his timely criticism and encouragement, and for being a constant source of ideas and inspiration. I owe him a very great debt indeed. In the construction of equipment, Mr. H. Johnson, Mr. M.J. Felthouse and Mr. R.F. Cartwright gave desperately needed technical assistance. Mr. Cartwright, in particular, was long-suffering, and I am grateful for his patience, good humour and willingness to help. Many people helped with discussion of various points, including Drs. E.F. Evans, P. Hammond, C.R. James and D. Regan, Mr. S.R. Yates, Mr. S.R. Hakiel, Mrs. V. MacKay and Miss M. Young. Mr. Hakiel in addition provided the original computed programme for data analysis and Mrs. V. MacKay has allowed me to refer to unpublished results.

I am indebted for the many hours of experimental time given by the voluntary, unpaid subjects. This research owes much to their patience.

Judy Milsom has provided much support over the last few years, and has helped towards the preparation of this thesis in more ways than can be easily catalogued. It is a pleasure to acknowledge this, and also the help given by my parents at all stages in my education.

Miss H.O. Henry has done an excellent job of typing up the manuscript. She has coped with many last minute alterations and has assisted in ways not normally required of someone typing a research thesis. She has my sincere thanks.

I would like to thank the Department of Clinical Neurophysiology at the Hospital for Sick Children, London, for the use of computer facilities.

The S.R.C. provided a Research Studentship, and I am grateful for their financial support.

CHAPTER 1 THE MCCOLLOUGH EFFECT

1.1 Introduction

In the late 1940's and early 1950's a number of research workers concerned with the problem of visual pattern recognition suggested that the visual system of animal and man seeks out and selects regularities and consistencies in the visual environment. It was argued that there may be functional sub-systems in perception concerned with the abstraction of features of high informational value, such as contours and changes in contour orientation (Hebb, 1949; Attneave, 1954). A few years later, Hubel and Wiesel (1959) presented some of the first neurophysiological evidence for such a feature-extraction process. They discovered classes of neurones in the visual cortex of the cat which can be excited by specific stimulus features such as a bar (line of contrast), its orientation, field position, length, axis and direction of movement.

The work of Hubel and Wiesel provided a springboard in visual neurophysiology, much subsequent work being concerned with the definition of "trigger features" for cortical sensory neurones. These investigations have in turn provided a major stimulus to visual psychophysics, resulting in an area of experimentation aimed specifically to examine whether contour processing units with similar tuning characteristics could exist in the human brain. Such supportive evidence was indeed soon discovered (Andrews, 1965; Campbell & Kulikowski, 1966). The close interaction between the two disciplines has led to the discovery of new psychophysical phenomena, proposals concerning excitatory and inhibitory processes which might operate within and between the feature-selective channels assumed to exist in the human visual system, and to new postulates for possible trigger features of cortical neurones in animals.

1.2 The McCollough Effect

One such proposal and line of research followed from a perceptual demonstration by Celeste McCollough (McCollough, 1965). Although it was assumed at that time that the human visual system does contain edge-detector mechanisms, no suggestion had been made that these showed any colour specificity. McCollough allowed her subjects to inspect for about 4 mins. a vertical grating viewed through an orange filter alternating with a horizontal grating viewed through a blue filter. Subsequently, subjects with normal colour vision reported that vertical and horizontal black and white gratings appeared tinted with the hue complementary to that originally paired with each orientation (e.g. in this situation, the vertical grating appeared green and the horizontal grating appeared pink). McCollough inferred two things from these results. Firstly, these edge-detector mechanisms must be colour-coded. Secondly, they are subject to adaptation, responding with decreased sensitivity to those wavelengths with which they have recently been most strongly stimulated.

McCollough considered many of the issues which were subsequently to absorb researchers, and it will be convenient to review these briefly in the context of her original paper. Firstly, there is strong evidence that the effect is not an ordinary after-image. Its generation does not require steady fixation or an intense stimulus. The colours remain stationary as the observer shifts fixation within the test pattern and can best be seen on grating patterns rather than a plain white surface (unlike ordinary after-images). Moreover, the colours are not as saturated as normal after-images and can be seen even after exposure to complementary colours.

Secondly, there is clearly a close linkage between the colour and the orientation of the stripes. Rotation of either the head or the achromatic test grating through 45° causes disappearance of all subjective colours and rotation through 90° causes the subjective colours to exchange places. Longer exposures cause these after-effects (A/E) to show up on other patterns, such as concentric circles, spirals, radiating lines or simply on chalk lines drawn on a blackboard, the colours being most predominant on those orientations closest to those used in the original inspection sequence. Finally, adaptation to patternless colours does not give rise to the McCollough A/E, in so far as one can tell from tests based on subjective reports of the A/E colours seen on an achromatic test card.

Thirdly, McCollough (1965) considered the question of interocular transfer of the A/E. One eye only was exposed to the alternation, as described. Immediately following this, the other eye was exposed to the opposite colour and orientation pairings. On subsequent testing, reports of colours seen on each orientation with the left eye were consistently the reverse of those seen with the right eye. The inference is that the eye channels are largely independent with respect to the orientation-contingent colour A/E, so that the edge detector mechanisms assumed to underlie the effect must be at a stage in the uniocular pathway prior to the level of binocular interaction.

1.3 The McCollough Effect: Experimental findings

McCollough (1965) proposed that the physiological basis of the effect is adaptation of colour-coded edge-detector mechanisms. Much of the reported research has been motivated by this hypothesis, and has attempted to demonstrate that some feature of the A/E is consistent with established characteristics of cortical physiology. While there is practically no evidence regarding adaptation of cortical units (e.g. see Stone & Freeman, 1973; I am also grateful for discussions with Drs. P. Hammond & C.R. James on this point), a great deal of evidence has been gathered which is consonant with the known spatial tuning properties of cortical neurones in cat and monkey. These results make it likely that such units exist in the human brain and are at least involved in the generation of the A/E. They do not necessarily support the idea that such orientationally-tuned units are also colour-coded, or that the mechanism underlying the effect is a depression of their sensitivity to those wavelengths to which they are assumed to be most responsive. However, it will be convenient at this stage to review this literature according to the parameters manipulated, and to point out how consistent the data is with single unit findings. The evidence which presents difficulties for the 'double-duty' and 'adaptation' hypothesis will be considered later.

1.3.1 Orientation Parameters

Orientation selectivity is a prime characteristic of the majority of neurones so far studied in the visual cortex of cat and monkey. Both simple and complex cell types show a high degree of orientation tuning for contours located in the discharge centre. As the orientation is varied from the optimum, response falls-off, usually failing long before an angle of 90° to the optimum is reached. Most field orientations could be specified to within 10-15° in cat and 5-10° in monkey (Hubel & Wiesel, 1962, 1968). This specificity seems to be due to the spatial summation of excitatory and inhibitory components (particularly along the line of optimum orientation) and not upon the sequence in which the underlying components are brought into play (Henry, Bishop & Dreher, 1974).

A number of reports have indicated that orientation is a critical parameter in pattern-contingent chromatic A/E, and attempts have been made to estimate the orientation tuning of these effects.

(a) Colour A/E made contingent on pattern

Fidell (1970) argued that if the human visual system contains neurones tuned to a particular orientation and colour, the orthogonally-oriented coloured gratings in the McCollough adaptation sequence would each maximally excite a different population of units. Fidell showed that if the adapting orientations were always at 90° to each other, A/E could always be established and did not appear to vary in strength with the absolute orientation of the lines. However, when a vertical grating was paired successively with one at 45° and then at 22°, reports of coloured A/E became less frequent. When the orientations were separated by only 11° hue reports were very rare. The assumption was that at this separation a single orientation population was stimulated.

MacKay and MacKay (1977) have shown that it is possible to generate A/E to one or a number of orientations simultaneously. The strength of A/E built up to a single orientation has a bell-shaped angular distribution, its strength falling to half-value at about 25° away from the inducing orientations. It is possible to associate the same colour with two orientations at right angles without mutual cancellation. Multiple A/E show independent time-courses of decay, and can be induced and retained for at least 8 orientations at once. With separations of 15° between the orientations of inducing stimuli, the induced A/E are barely significant. This latter finding is consistent with the results of Fidell (1970).

Finally, MacKay (1970) and Campbell and Howell (1972) have reported that if two orthogonally-oriented and differently coloured gratings are optically superimposed on a screen, the appearance of the pattern continuously changes, sometimes one being seen and then the other. The effect can be seen with monocular viewing thus ruling out binocular rivalry as an explanation. The orientation of the gratings is critical, the alternation not being apparent until the angular separation is 15°-20°. It has been argued that for alternation to occur the gratings must excite two separate sub-populations of neurones, and this only occurs when the gratings are separated by this minimum angle.

(b) Pattern A/E made contingent on colour

Other researchers have reversed the role of colour and pattern and shown that a figural A/E can be made contingent on colour. Held and Shattuck (1971) utilised the tilt A/E. Subjects were exposed to alternating red and green gratings, each tilted 10° off vertical but in opposite directions. Subjects then viewed a vertical test grating coloured red in the top half and green in the bottom half. All subjects showed a shift in their judgement of perceived straightness, so that the test bars appeared tilted in the direction opposite to that of the adaptation pattern with the same colour. Further, an attempt was made to judge the magnitude of the effect as a function of the angle between adaptation and test patterns, which they argued should give some indication of the breadth of tuning of the detectors involved in producing the A/E. Test patterns were always vertical, while on successive occasions the adapting patterns were varied between 0° and 75°. The strength of the effect peaked at an adaptation tilt between 10° and 15° and was zero at 0° and 45°.

1.3.2 <u>Space Frequency Parameters</u>

Neurophysiological work in this area followed from psychophysical studies which showed that adaptation effects following exposure to an achromatic sine-wave or square-wave grating were restricted to a narrow frequency range around that of the adapting grating (Blakemore & Campbell, 1969). Campbell, Cooper and Enroth-Cugell (1969) have shown that cortical units, as well as geniculate cells, show a specificity in response, spike count for a particular unit depending on the space frequency of the stimulus grating. The optimum stimulus (orientation, space frequency, etc.) was used for each unit studied in detail. The variations in the low frequency end of the curve prevented any meaningful analysis, but the high frequency end showed a sharp cut-off in all cases. Optimum frequencies ranged from 0.18-1.6 cycles per degree. Any given unit responded to a grating ± 1 octave from the optimum frequency.

A number of studies have shown that space frequency is an important parameter underlying pattern-contingent colour A/E, and there are similarities in the bandwidth of the effect with those obtained using achromatic gratings in human subjects and with responses of single units in animals.

(a) Colour A/E contingent on pattern

Stromeyer (1972) exposed subjects to one of a number of coloured gratings with space frequencies in the range 1 to 20 cycles per degree and tested with that and all others in the set. Testing with gratings of the appropriate colour, it was found that A/E were strongest when the space frequency of the test and adapting pattern was the same, and became progressively weaker on test patterns of higher and lower frequency, but effects were still detectable 2 or 3 octaves either side.

A/E cannot be established to two patterns of different colour but the same orientation unless their space frequencies differ. Breitmeyer and Cooper (1972), using the colours red and green, combined a 3.3 cycle per degree vertical grating of one colour with vertical gratings of the complementary colour and various higher frequencies over a range of 2 octaves. The number of reports of colour A/E on achromatic gratings increased with increase in the difference between the space frequencies of the gratings of the adapting pattern. Colour reports were zero when the two patterns had the same space frequency, or when they differed by only 0.5 cycles per degree, to 100% when they differed by 2 octaves. Lovegrove and Over (1972) have confirmed that it is relatively easy to induce a colour A/E when the two adapting patterns differ by an octave or more. In addition, they showed that at least one of the patterns must have a space frequency greater than 1.5 cycles per degree. May (1972) has shown that thresholds for detecting a coloured grating are raised only when the adapting and test stimuli have the same frequency and colour.

Uhlarick and Osgood (1974) attempted to separate out the relative influence of bar width, slit width and spatial frequency. They concluded that black bar width had the major influence on strength of the A/E and suggested that the neurophysiological mechanism underlying the McCollough Effect might consist of orientation specific units that are specific to the widths of bars (rather than the space frequency of the pattern) and the chromatic characteristics of the surround.

(b) Pattern A/E contingent on colour

Virsu and Haapasalo (1973) have reported a space frequency shift effect based on a colour difference. Subjects adapted to a red 7 cycle per degree grating alternating with a green 2.5 cycle per degree grating. Each was split into halves, one above and one below a fixation mark. A 4 cycle per degree test grating was similarly split around the fixation mark, one half being coloured red and the other half green. The space frequency of the two halves appeared to differ, the half coloured red appearing to be of lower frequency to that of the green half.

1.3.3 Colour Variables

In view of McCollough's original suggestion that the A/E is evidence for the existence of colour-coded edge-detectors in the human visual system, one question of considerable interest is whether there are units in the visual cortex of cat and monkey which show precise tuning for colour in addition to specificity for shape and orientation of the stimulus pattern. If so, what are the colour properties of these units? At the present time there is no evidence for such units in the cortex of the cat, but there is for monkey.

Hubel and Wiesel (1968) were specifically looking for such units, and indeed expected to find them considering the large number of LGN cells having colour-opponent properties. However, they found very few which showed any marked preference for wavelength - for a high proportion of cells the response to a given stimulus was quantitatively the same regardless of wavelength, and the optimum stimulus shape was independent of wavelength. This was confirmed in penetrations in the foveal representation of the visual cortex. Of the 25 simple cells recorded in rhesus monkey, 6 (25%) had more specific colour-coded properties, the inhibitory and excitatory parts of the field differing in spectral sensitivity in the manner of geniculate Type I cells. All six were similar in organisation, having a long narrow excitatory region with highest sensitivity to long wavelengths, flanked on either side by more extensive inhibitory regions with relatively greater blue-green sensitivity. These cells behaved as though they were receiving input from a set of Type I red 'ON'-centre, green 'OFF'-surround geniculate cells, the commonest type found in dorsal geniculate layers.

177 complex cells were encountered, and of these only 13 (7%) were identified as having clear colour specificity. Four gave responses to coloured stimuli that were qualitatively similar to their response to achromatic stimuli, but only over an unusually restricted band of wavelengths. A cell might respond actively to the blue-violet (or red),

but not to light at the other end of the spectrum. Six responded actively to a properly oriented slit at some wavelengths but not others, and gave little or no response to a similarly oriented white slit at any intensity. Five of the six had 'ON' responses favouring long wavelengths. Three had similar opponent-colour properties but had hypercomplex feature properties.

In total, only 10% of their sample had colour-opponent properties. Boles (1971) and Poggio (1971) reported a higher proportion.

In most studies of the McCollough Effect, hue has not been manipulated as an independent parameter. Red and green have been the colours most commonly used. McCollough (1965) used orange and blue-green, but reported that practically any colours would do. Stromeyer (1969) carried out a study in which colour was the independent variable. His purpose was to determine which colours would generate an A/E and the hue and relative strengths of the resulting A/E. A variety of colours were used, but were paired with only one adapting orientation. Testing was carried out using achromatic gratings of the same and orthogonal orientations, and subjects were required to report the hue of the A/E and its strength according to a scale of measurement. A/E reports were only accepted if the hue showed reversal when the pattern was rotated through 90°. The A/E produced by red and blue-green were the strongest, and were predominantly green and pink respectively. The A/E associated with violet and blue-green were generally weak, the A/E colours being mainly green and pink. These A/E hues could also be induced by reddish-yellow and greenish-yellow filters, respectively.

Fidell (1970) and May (1972) have used different methods to estimate the strength of the A/E to each adapting colour. Fidell required subjects to adjust the colorimetric purity of the test grating while May estimated the elevation in threshold for detection of the red and green gratings. Fiddell found that A/E strength was greater following adaptation to green gratings - that is, the red A/E was more vivid. By comparison, May found that thresholds for red test gratings were higher than those for green test gratings, so that in this case the red adapting gratings had the strongest effect.

Cosgrove et al (1974) utilised stabilised image techniques in studying the interactive effects of pattern and colour. In the first experiment a coloured line was stabilised on the retina, and the temporal characteristics of the subsequent fading were observed over the next 20 min. The colour of the line was then rapidly switched to that of its complementary. It was found that there was an immediate decrease in the 'fade time' of the image, and the subsequent process of 'degradation' of the image followed the same time course as the pre-substitution period. The implication was that a separate mechanism was being adapted following the chromatic substitution. In the second experiment it was shown that the time taken for the re-appearance of a line which had just faded was shorter when there was a chromatic substitution and the colour was different to the post-substitution colour. Finally, it was shown that after adapting to a coloured grating the fade time of a stabilised line was greater when the colours of the grating and line were the same.

1.3.4 Interocular Transfer

Neurophysiological studies have shown that some cells in the visual cortex of cat and monkey are driven exclusively by stimulation of one eye, but that the majority respond to correctly located stimuli in either eye. For these cells, all shades of monocular dominance have been found (Hubel & Wiesel, 1962, 1968, 1977; Brooks & Jung, 1972). Psychophysical studies of interocular transfer of adaptation effects have been carried out with the aim of determining the site of adaptation. Non-contingent A/E usually show a high degree of transfer to the non-adapted eye (Gilinsky & Doherty, 1969; Blakemore & Campbell, 1969), and this has been taken as evidence that the site of adaptation cannot occur prior to the site of binocular interaction. There is now substantial evidence that the McCollough Effect does not show this transfer and so the site of adaptation must be largely within the monocular pathway. This evidence is reviewed in more detail in Appendix B of this thesis.

1.3.5 Retinal location specificity and importance of eye movements

Some other features of the A/E are difficult to relate to specific neural mechanisms. Harris (1969) and Stromeyer (1969) have shown that the A/E can be confined to restricted parts of the retina. In Stromeyer's study, subjects fixated a point in the centre of an 8° square which could be illuminated alternately by red and green orthogonally oriented gratings. Following this, the fixation mark was moved and the subjects asked to report on the degree of saturation of the test pattern. Reports of the strongest saturation occurred when the retinal locations of the adapting and test patterns approximately coincided. Further, it was found that if the edge of the test pattern was moved by as little as ½° away from the adapted area, it appeared colourless. Harris showed that adjacent areas of the retina could be adapted to opposite pairings of pattern and colour. Both authors concluded that the A/E could not be related to units that had large receptive fields.

The importance of eye movements have been studied by two groups. Piggins and Lepmann (1973) stabilised the adapting patterns on the retina by means of a contact lens technique. The pattern became degraded after 4-6 secs after which time the field illumination was switched on and off intermittently. No McCollough A/E were reported, though the same subjects gave reports of clear A/E when allowed to inspect the inducing patterns in the normal way. By comparison, Stromeyer (1974b) found that subjects gave consistent reports of weak McCollough A/E when the stimuli were sine wave gratings flash-presented for 9 msecs. every second and repeated 2000 times. Based on other findings, he pointed out that eye movements greater than 1' arc are highly unlikely when the subject is voluntarily fixating a target and stimulus exposure is less than 10 msecs. He further reported that quite vivid A/E could be established to square wave gratings even though flash presentation was for only 60 μsecs and there were only 200 presentations, each presentation being separated by a 2 secs. dark period.

1.4 Temporal Parameters: An Uncharted Area

At the time of commencing this research project in October 1973, only two papers had been published in which the factor of time had been an independent parameter. One was that by Stromeyer (1974b), already discussed, which showed that A/E could be established even by very brief stimulus exposures. Hajos (1968)* carried out a brief investigation regarding temporal parameters of stimulation on strength of the A/E. Subjects were adapted in the usual way, with intermittent periods of testing on achromatic gratings. When the subject had made six successive reports that an A/E was visible, this was taken as the criterion for establishment of the A/E. The number of 'reverse' presentations to neutralise the original effect was taken as a measure of the strength of the original

---

*I am grateful to Mrs. V. MacKay for helping with a more extensive English summary.

effect. Three points emerged. Firstly, strength was proportional to the duration of exposure for a constant light time relation. Secondly, the discrete period of exposure of the stimulus pattern had no effect over the range 0.5 to 4 secs. Finally, the length of the dark interstimulus period did have an effect. Adapting with stimulus periods of 1 sec. and 2 secs., the strength of the A/E increased as the interstimulus period was lengthened (0, 0.5, 1 and 2 secs.).

This brief report does indicate that the temporal parameters of stimulation can affect the strength of the induced A/E. This idea has not been followed up in any published reports known to this author. Indeed, at the end of 1975 Skowbo et al., in a review article, asserted that "The rate at which the adapting patterns alternate does not seem to be of crucial importance for stationary grating effects" (p.504). Certainly, it does seem that A/E can be built up over a wide range of temporal values for both the stimulus presentation and the dark interstimulus period.

The work to be reported in Chapters 3, 4 and 5 and Appendix A arose out of a suggestion made by Professor D.M. MacKay that a study of these parameters may yield further insights into the mechanism which underlies the McCollough Effect.

CHAPTER 2: EQUIPMENT AND METHODOLOGY

2.1 Introduction

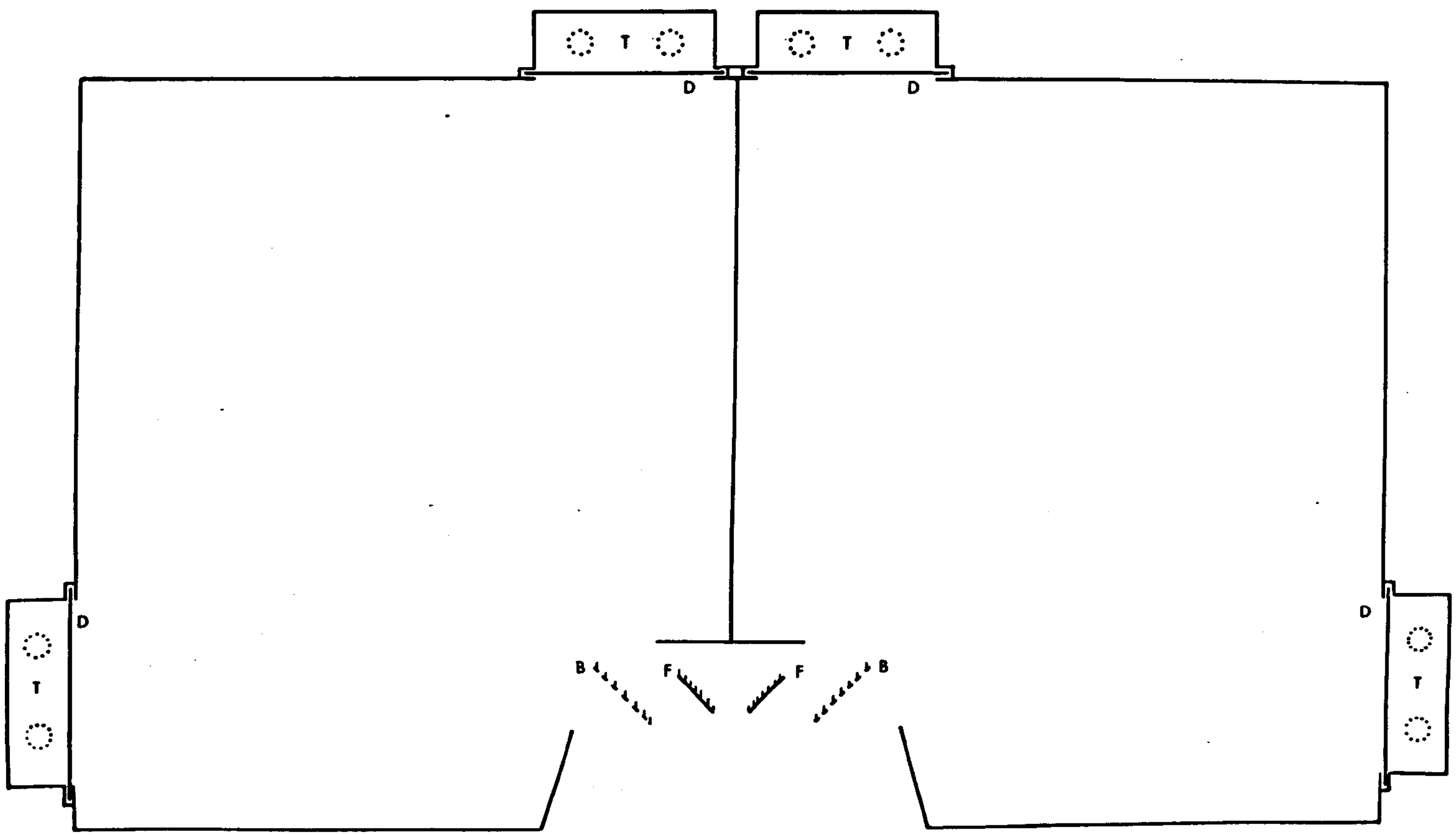
For some time members of this Department had been actively researching into certain aspects of the McCollough Effect. During the early phase of this project the available facilities proved adequate for appropriate pattern and colour stimulation and for providing a measure, in arbitrary units, of the strength of induced A/E. However, at a later stage improved equipment proved necessary to provide more precise control over the period of exposure of the stimuli. The apparatus used for measuring the strength of the A/E was the same throughout the course of the project.

2.2 Pattern Stimulation Equipment

2.2.1 Slide projectors

The arrangement of the equipment was as follows. The subject sat with chin supported and head upright, approximately 110cm. directly in front of a projection screen. Two projectors were mounted on a stand located slightly above the subject's head. Each projected an image, 32cm. x 20cm. in size at the screen, of a left-oblique or right-oblique square-wave grating pattern. The angular size of the field subtended at the eye was 16° x 10°. Each grating consisted of 42 black and white stripes, giving a space frequency at the eye of approximately 2.5 cycles per degree. One pattern was projected through red (590-670nm) and the other through green (480-560nm) "Cinemoid" filters. The luminance of the coloured stripes were matched at approximately 0.6 Log Foot Lamberts. An electronically controlled flap could be moved in front of each projector lens to allow alternate exposure of the patterns. Timings of

FIG. 2.1



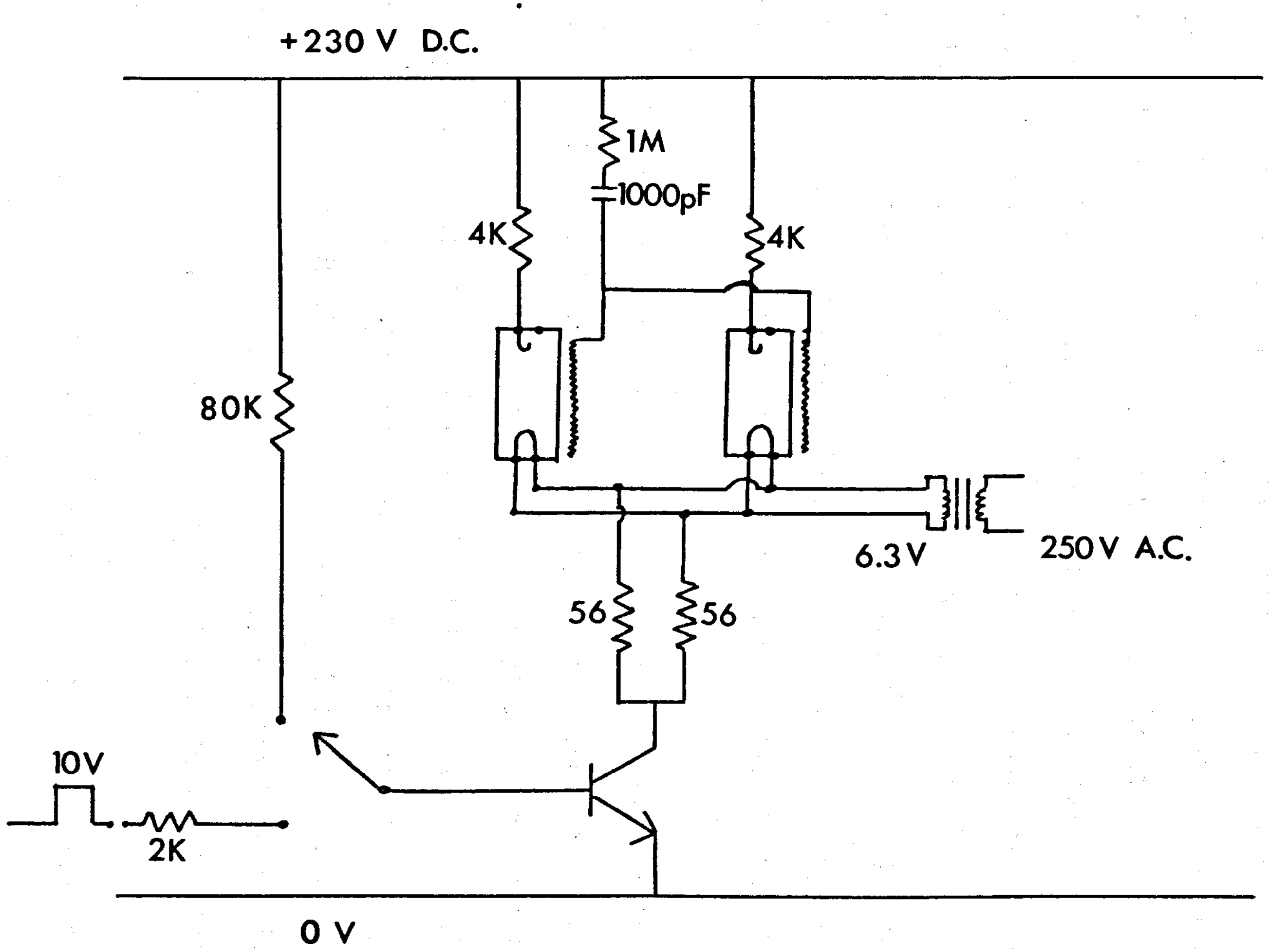
D, Perspex diffuser; B, Beam-splitter; F,Front-surface mirror; T, Fluorescent tube exposure and darkness were regulated by monostable circuits.

2.2.2 Tachistoscope

The arrangement of this apparatus is shown in Fig. 2.1. The framework consisted of "Dexion" slotted steel securely mounted on a hardboard base. The sides were covered with black card, with four apertures for the stimulus fields. Metal slide guides were used to retain the fluorescent tube boxes and a "Perspex" diffusing screen, and to accurately locate the pattern frames. Pattern frames were made from thick black card with a window 10.5cm. square (12° x 12° angular subtense at the eye). Grating pattern transparencies were attached to the window of each of the four frames, so that the black-and-white stripes were exactly aligned. Each grating consisted of 26 black and white stripes of approximately equal width, giving a pattern of space frequency approximately 2¼ cycles per degree at the eye. Appropriate numbers of colour interference and neutral density filters could be inserted behind the pattern frames and the "milk-white" diffusion screen ensured uniform illumination of the entire field. Fixation circles, with a diameter equal to the width of five grating bars, were scratched into the surface of two pieces of clear perspex. When located in the appropriate eye fields these circles were optically superimposed. Edge-illumination of the perspex with a low voltage bulb caused these circles to "glow".

The fields were optically superimposed by the arrangement of front surface mirrors and beam splitters shown in the figure. The front surface mirrors were cushioned with a piece of thin foam, and plastic screws at the front allowed fine adjustment of the angle. The beam splitters were mounted in a framework which permitted rotation in the horizontal and vertical planes. These facilities allowed correct alignment of the

FIG. 2.2 CIRCUIT TO DRIVE TWO FLUORESCENT TUBES



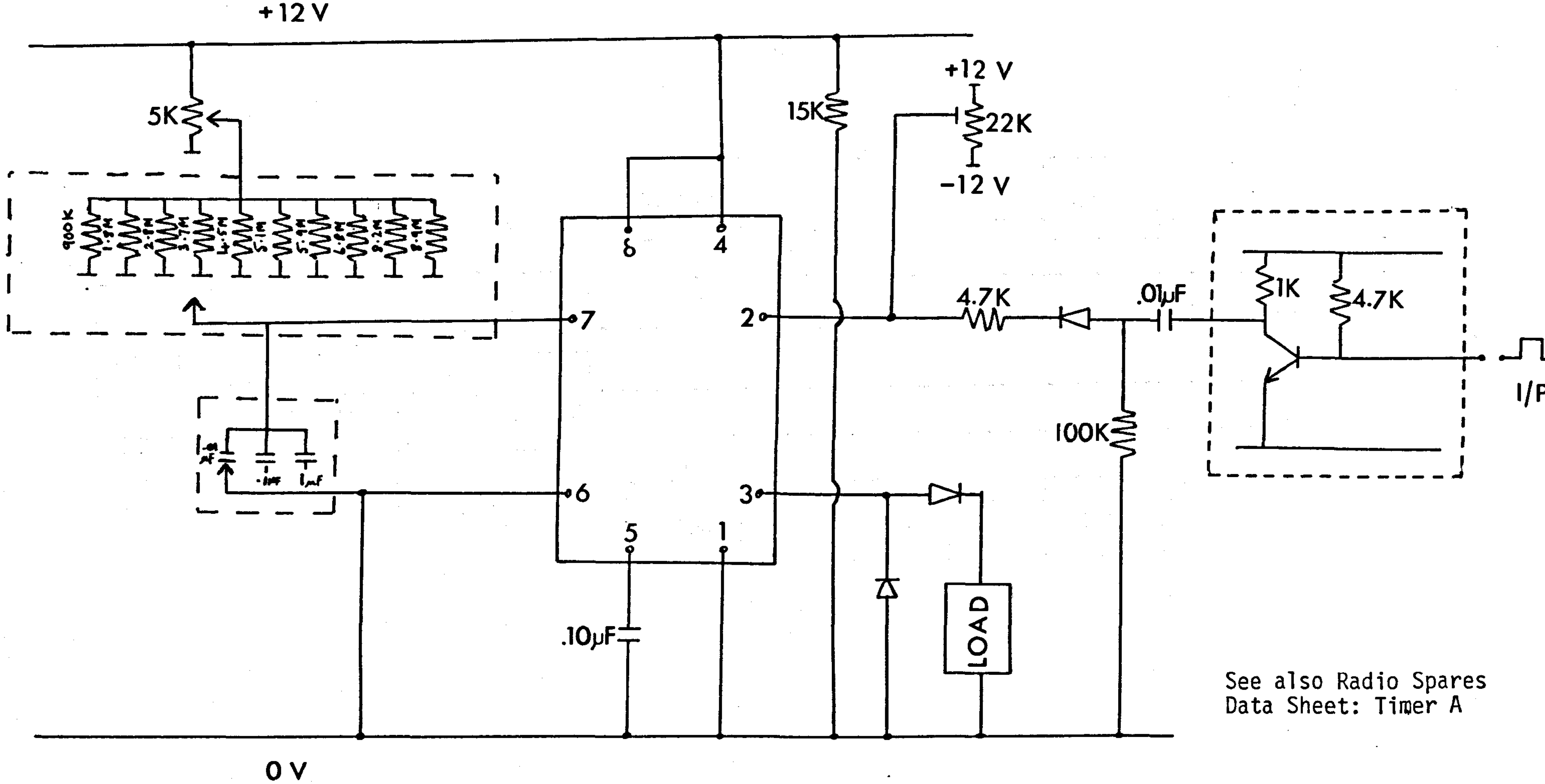
patterns. The beam splitters transmitted and reflected light in approximately equal proportions. A black card located behind the front surface mirrors prevented direct view of the fields immediately in front of each eye, and a central dividing screen restricted light scatter within the apparatus.

Each field was back-illuminated by two fluorescent tubes (54VL 'Daylight'). The drive circuit shown in Fig. 2.2 controlled the current supply to these tubes. This circuit was triggered by monostables made from integrated circuit chips, as shown in Fig. 2.3. Each monostable provided a 10 volt square wave pulse, the length of which could be varied from 10msec to 20sec by means of switching resistors and capacitors. Repeat accuracy was within the range ± ½% to ± 2%, accuracy being greater for shorter duration output pulses. The duty cycle was controlled by two outputs from a Wavetek Function Generator, the output pulses being 180° out of phase.

Six monostable circuits were available, and the triggering arrangement of these is shown in Fig. 2.4. Monostables 1, 3 and 5 were controlled by the cycle from output A of the Wavetek, and monostables 2, 4 and 6 from output B. A waveform discriminator in the input lines to the monostables selected the positive-going edge. Circuits 1 and 3 were triggered simultaneously, as were circuits 2 and 4. Circuits 5 and 6 were triggered only indirectly, by the output from circuits 3 and 4 respectively. This arrangement provided "delay" facilities for the triggering of one field relative to another.

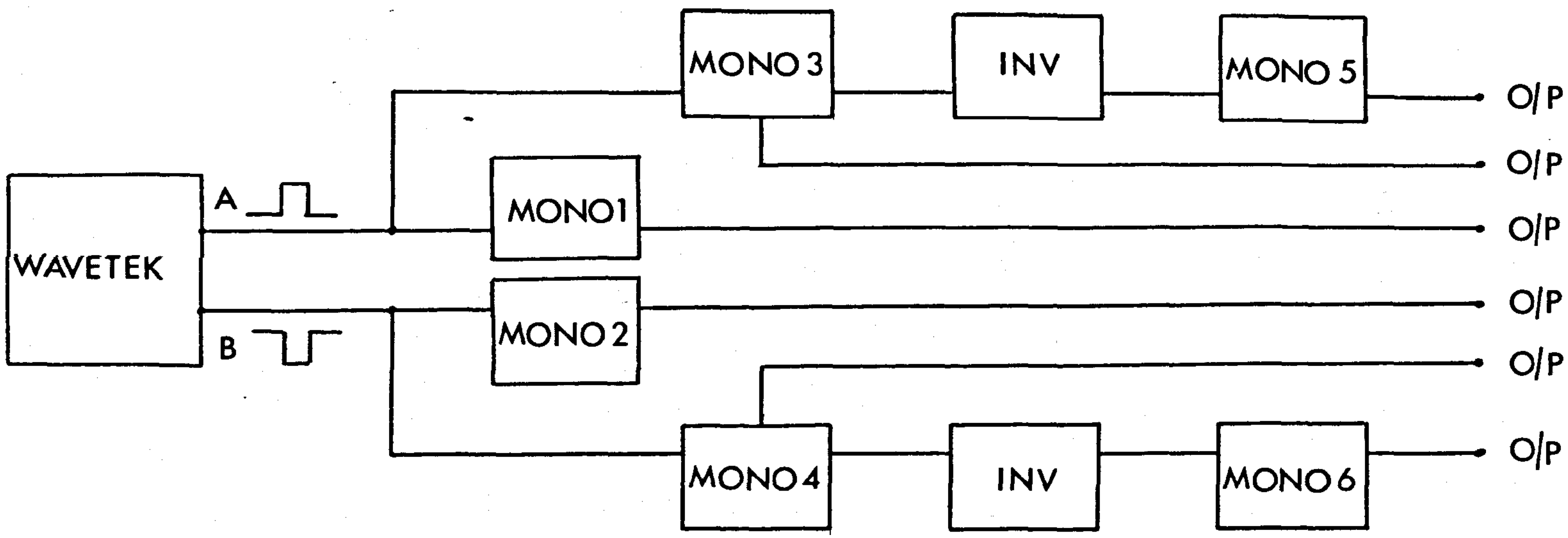
Wavelengths of Cinemoid filters and luminances of fields were as defined for the previously described equipment.

FIG. 2.3



See also Radio Spares
Data Sheet: Timer A

FIG. 2.4


WAVETEK
A
B
MONO 1
MONO 2
MONO 3
MONO 4
MONO 5
MONO 6
INV
INV
O/P
O/P
O/P
O/P
O/P
O/P

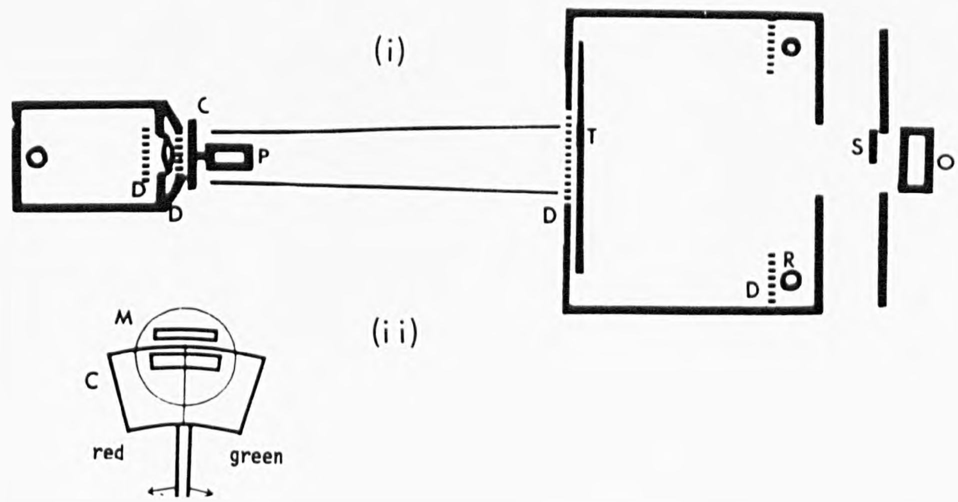
2.3 Measurement of A/E Strength

2.3.1 Apparatus

The apparatus (see MacKay & MacKay, 1973; 1975) is shown in Fig. 2.5(a), and the test pattern in Fig. 2.5(b). The pattern (15cm. x 15cm.) consisted of two orthogonally-orientated black and white gratings placed side by side, with a small rectangular translucent window (6.5cm. x 2.2 cm.) inserted into the centre of each. The entire pattern was illuminated from the front by an annular fluorescent tube ("Daylight") fed by stabilised direct current. The luminance was adjustable to match that of the rectangular windows. A lining of yellow paper on the walls of the lamp box assisted the matching of the slightly yellowish colour of the test window at neutral colour balance. Rear illumination of the centre windows was by a 100w. projector with a diffusion screen in the slide holder. A red and a green filter were attached by an extension arm to a pen motor and could be moved in front of a translucent aperture over the projector lens. This arrangement enabled the displacement of the red/green boundary (i.e. the excess of red over green, or vice-versa) to be linearly related to pen-motor current. A second aperture permitted desaturation of the beam by a fixed amount of white light (Fig. 2.5).

The current flowing in the pen-motor was controlled by the circuit shown in Fig. 2.6(a). This provided a parallel input to the Y axis pen shift circuit of an X-Y chart recorder, enabling the position of the marker pen to be controlled by a derived voltage. Movement of the armature of the pen motor was linearly related to movement of the marker pen of the chart recorder (see below). The switch arrangement shown in Fig. 2.6(b) permitted three baseline positions of the chart recorder marker pen, while the circuit in (a) permitted movement of the pen around that baseline. A two-way key controlled the pen drop onto the chart

FIG 2.5 a



(i). Apparatus to measure pattern-contingent chromatic aftereffects. (ii). Detail of adjustable colour filter as viewed from T. C, movable red and green filters; M, mask with slits over projector lens; P, pen motor; D,diffusing tissue; E, diffusing tube; T, test figure; R, ring lamp; S, shutter to cover either eye; O, chin rest. (From MacKay and MacKay, 1975).

FIG 2.5b

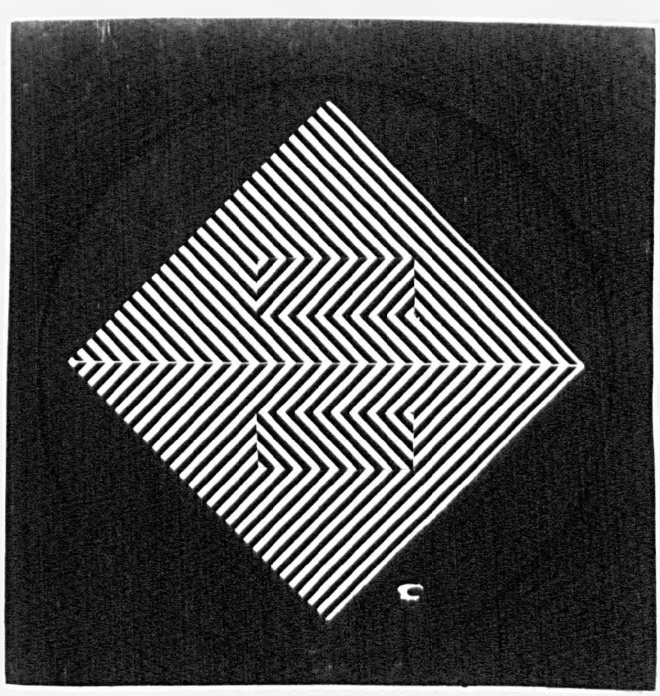


FIG. 2.6 b

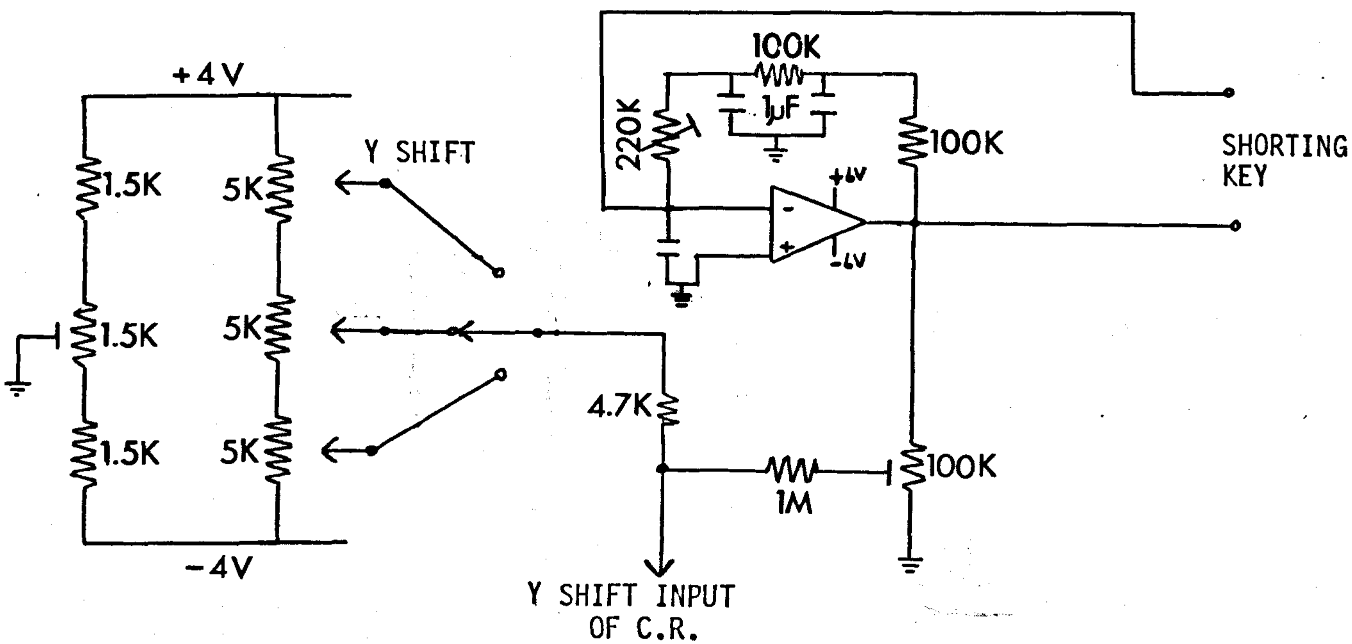
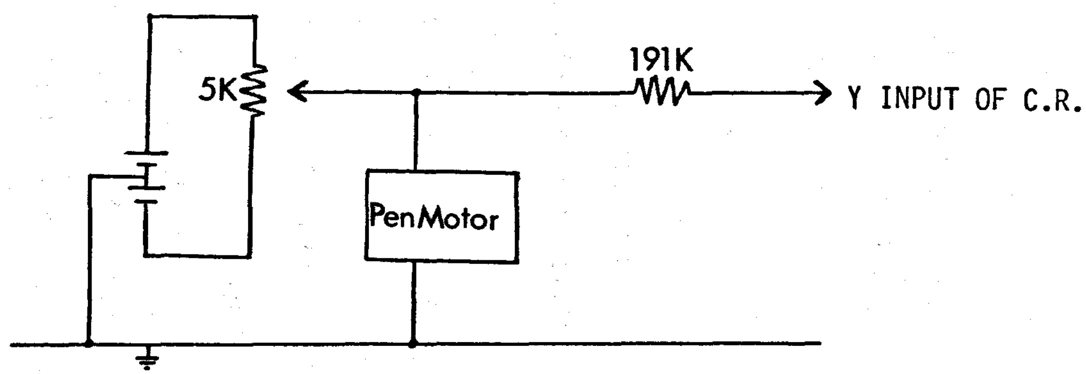


FIG. 2.6 a



recorder paper. One direction of movement of the key caused the pen to drop and leave a "dot" mark on the paper, while the reverse movement of the key caused the pen to drop and simultaneously activated an oscillator circuit, causing the pen to leave a small "dash" mark on the paper.

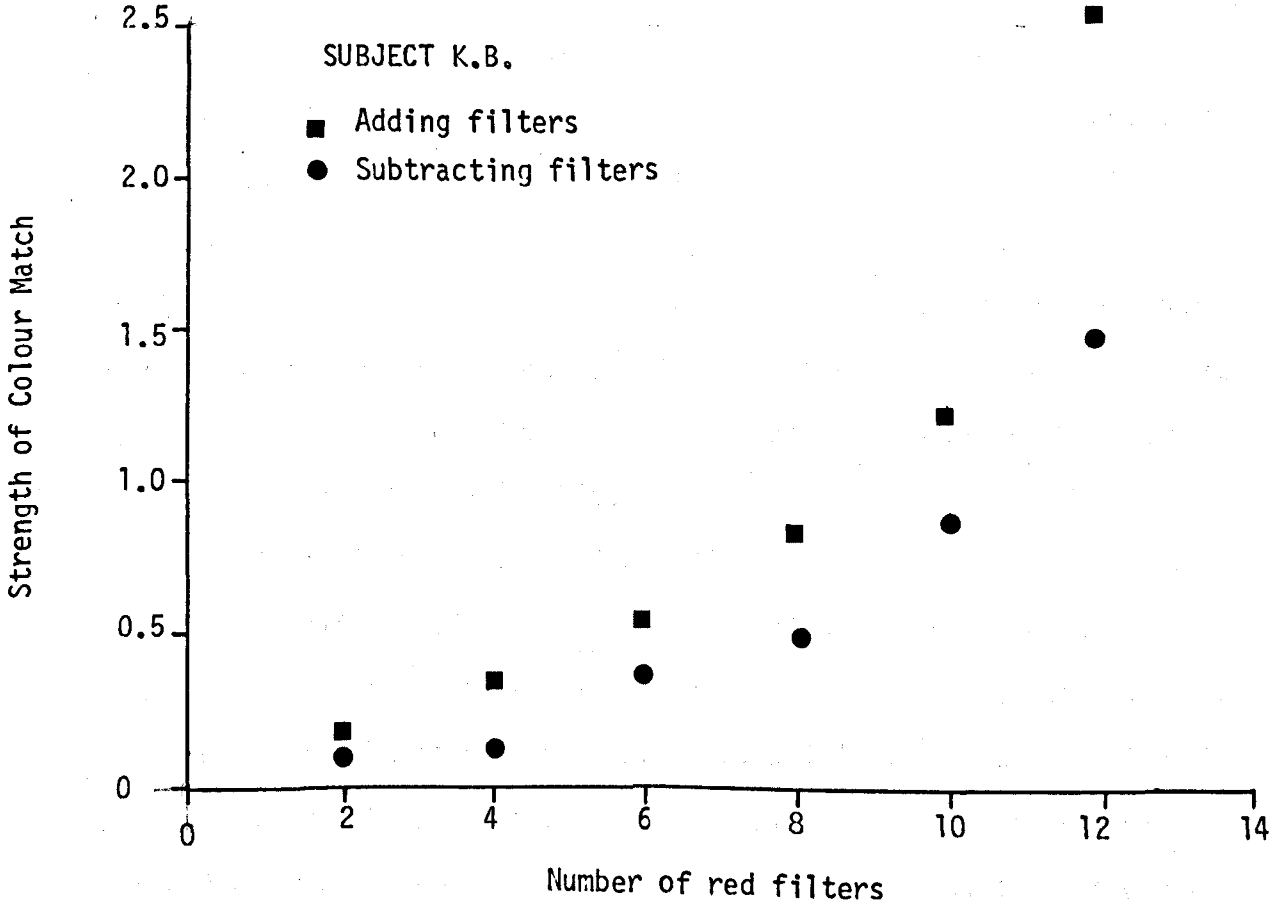
2.3.2 Calibration of Apparatus

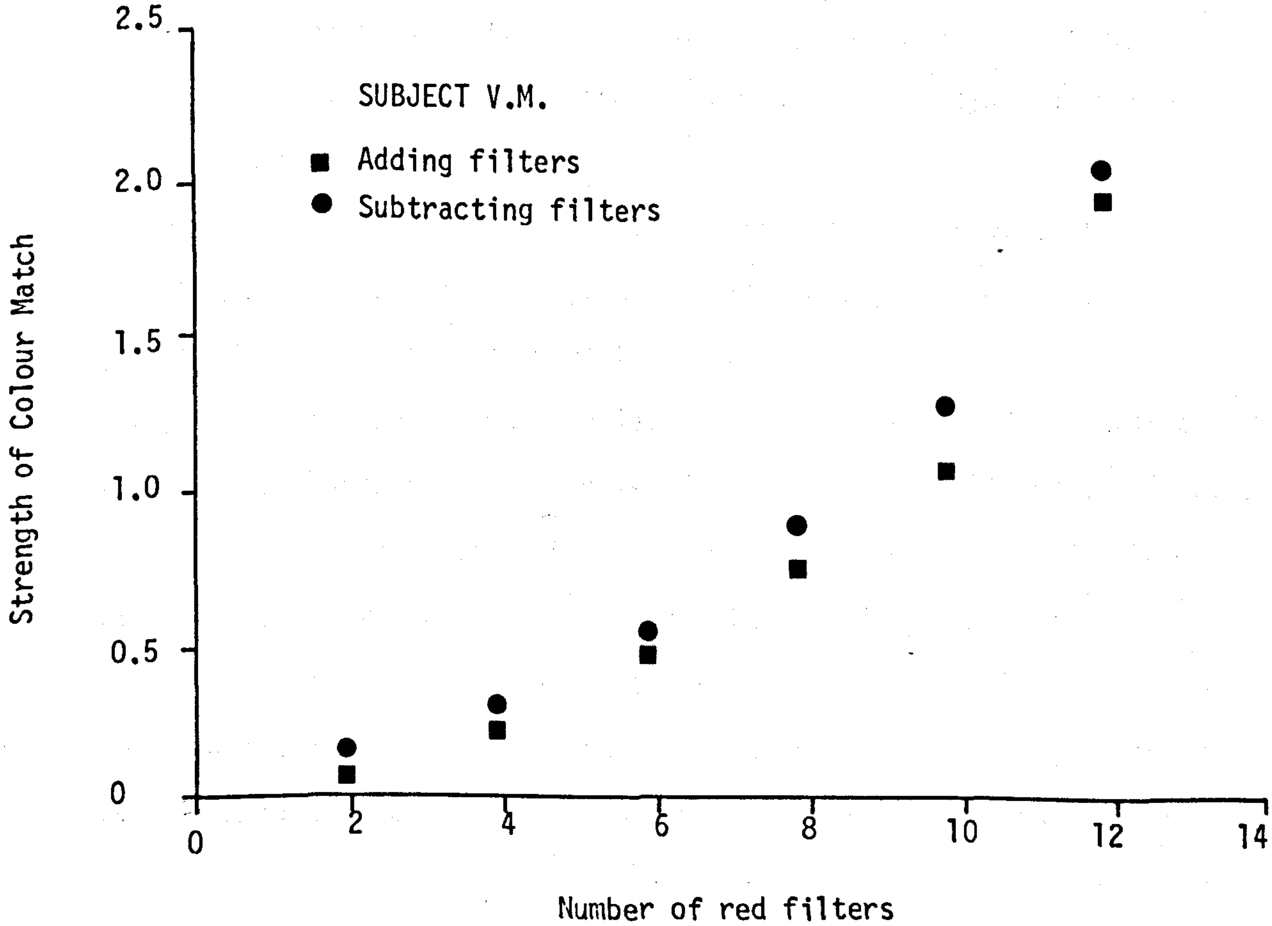
The testing apparatus essentially enabled the subject to match the perceived A/E by adjusting the colour bias of the centre window of the test card. Sensitivity and linearity of the equipment was ascertained by the following methods:

(i) Linear range

The resistances were chosen to provide a full scale deflection of the marking pen of 9cm. for full rotation of the potentiometer controlling the colour bias on the windows. However, the effective range of measurement was slightly less than this. The colour bias on the window was adjustable only while the red/green boundary between the filters (on the pen motor arm) did not extend beyond the edge of the beam from the projector. The filters were so arranged that the boundary passed outside the edge of the projector beam for full armature deflection, but with sufficient overlap of the filter at the other side to prevent additional white light desaturating the beam. The effective linear range was therefore the distance moved by the chart recorder marker pen as the red/green boundary passed from one edge of the beam to the other. This range allowed 7cm. pen movement. In practice, it was found difficult to measure A/E as strong as this because very often the measurements were "slewed" - each adapting colour induces a different strength of A/E (which varies from subject to subject) and this may result in the measurement going beyond the linear range for one direction of pen movement.

FIG. 2.7


SUBJECT K.B.
Adding filters
Subtracting filters
Strength of Colour Match
0
0.5
1.0
1.5
2.0
2.5
0
2
4
6
8
10
12
14
Number of red filters


SUBJECT V.M.
Adding filters
Subtracting filters
Strength of Colour Match
0
0.5
1.0
1.5
2.0
2.5
0
2
4
6
8
10
12
14
Number of red filters

(ii) Linear relationship between displacement of chart recorder pen and pen-motor arm.

The relationship between increases in the colour bias on the window and movement of the marker pen on the chart recorder was investigated. A rule was located over the filters by means of a clamp and stand. The displacement of the red/green boundary was then measured for each 1cm. movement of the recorder pen. Equal movements of the pen were found to be associated with approximately equal displacements of the boundary, indicating a linear relationship.

(iii) Sensitivity of the colour adjusting system

The sensitivity of the system controlling colour was checked throughout the entire range. The calibration procedure consisted of rotating the subject's control knob through 10° steps and measuring the displacement of the pen motor arm. The relationship was non-linear: equal angular rotations produced large displacements at the extreme ends, which became progressively less as the arm approached the centre.

The equipment was therefore most easily adjusted in the central portion of the range.

(iv) Relationship between colour match and colour of test card

The ability of the equipment to deal equally well with all strengths of A/E within its range of sensitivity was investigated by studying the variation in the colour match relative to the surround of the test card. Subjects, who were assumed to have no orientationally-linked colour bias, made a normal colour match of the window against the surround. The redness of the surround was then progressively increased by equal steps by addition of strips of red filter to the annular tube illuminating the front of the test card, subjects repeating the colour-match procedure each time filters were added. This procedure was continued until the annular tube was completely covered, at which stage the colour saturation of the test card was much greater than any observed A/E, for one of the subjects at least (K.B.). The results for two subjects are shown in Fig. 2.7, an approximately smooth curve providing a good fit to the data points on all occasions. This monotonic function suggests that the equipment is equally sensitive throughout the measurable range of A/E strengths.

2.4 Experimental Procedure

This consisted of three phases:

(1) a pre-adaptation test condition checking for the presence of any colour bias linked to the orientations to be used in the adaptation period

(2) a prolonged period of exposure to alternation of orthogonally-oriented gratings of opponent colours

(3) a period following adaptation during which measurements were made of the strength of the induced A/E.

2.4.1 Pre-adaptation test

Experiments were conducted at a low level of room illumination. The subject adjusted to this level and was then seated in front of the measuring equipment. The test equipment was screened from room illumination, and room lights were out of the subject's direct line of vision. The subject sat with head upright and chin supported at a distance of 73cm. from the test pattern, which had a space frequency of approximately 2.5 cycles per degree. With neutral colour bias on the window of the test card, the subject adjusted the intensity of the achromatic illumination of the test pattern until a satisfactory match was achieved between the brightness of the window and that of the surround. The luminance of the white stripe was typically approximately 0.4 Log Foot Lamberts but within limits this had been shown not to be a critical factor (see MacKay & MacKay, 1975). The subject then fixated the test windows, each eye being exposed in turn by means of an adjustable patch. By rotating a smooth knob controlling pen-motor current, he then adjusted the colour bias on the window until this matched the perceived colour of the surround. The subject then recorded the current in the pen motor by pressing a two-way key connected to an X-Y recorder, as already described. The key was pressed one way for an upper window match and the other for a lower window match, causing different symbols to be associated with each orientation. The difference between the settings for upper and lower test windows was taken as a measure of the chromatic A/E observed. This procedure was repeated for each eye for each test window, the order of testing being: (1) left eye/upper window, (2) right eye/upper window, (3) left eye/lower window, (4) right eye/lower window. However, control runs established that the order of testing was not critical. This sequence was repeated four times. The complete testing sequence typically took about 1½ minutes. The average value for the two eyes was taken as a measure of the strength for that testing period. Any orientation-linked colour bias was subtracted from or added to the post-exposure readings, according to the relative polarity of the bias of the pre-test. Control procedures established that brief exposure to maximum colour bias on the window induced no measurable A/E (see Appendix A).

2.4.2 Adaptation procedure

Procedures using the tachistoscope were essentially the same as those using the projectors, and the former will be described. After the period of pre-testing, the subject sat comfortably at the tachistoscope with chin supported and head position adjusted to place each eye directly in front of the appropriate front-surface mirror, giving a view of the fixation circle. Two identical fields were then switched on briefly to confirm proper positioning of the head to view the whole of the field and to ensure correct fusion of the patterns.

After black-out of room illumination, the equipment was switched to automatic triggering mode. Each field could have pattern orientation and/or colour varied as required, and be illuminated with variable onset asynchrony and for variable periods. However, for normal stimulation two identical fields were triggered by the same monostable circuit, allowing simultaneous onset and offset of illumination of both eyes. Illumination of the other two identical fields was controlled by a separate monostable circuit, the alternation between the two circuits being controlled by the cycle duration of the Wavetek. The presentation period, length of interstimulus interval and rate of alternation were thus easily controlled. The particular orientation and colour pairings were easily altered by interchanging the colour filters between fields. For subject K.B., orientation/colour pairings were reversed each day for the experiments reported in Chapter 4.

During the period of exposure to this adaptation sequence the subject allowed his eyes to "wander" around the fixation circle in a constant direction. This procedure allowed equal exposure to the coloured and dark bars of the pattern and ensured standardisation of eye movement conditions amongst subjects. The duration of exposure was controlled by the experimenter. During adaptation, subjects were asked to make a verbal report on the appearance of the patterns and the occurrence of any afterimages, particularly during the dark interstimulus period.

2.4.3 Post-adaptation period

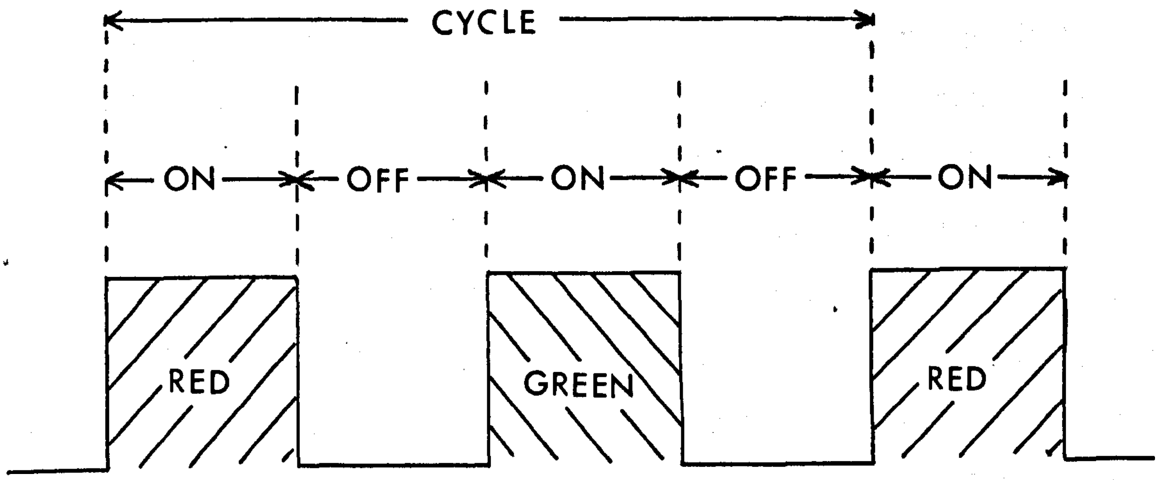
After the period of exposure, room lights were switched on and the subject returned to the testing equipment. After one minute of adjustment to normal illumination conditions, the first colour match was started. Testing was performed in the same order as for the pre-adaptation condition. After this first set of readings, the subject reported verbally on the appearance of the two halves of the test pattern. The testing procedure was repeated several times with progressively longer intervals between sessions. During the exploratory experiments, the subject was permitted to move around freely, returning to the laboratory only for the short periods of testing. This procedure allowed the whole process of decay to be determined with minimal inconvenience to subjects. However, a number of difficulties became apparent. Firstly, every environment exposed subjects to different light intensities, and also to other pattern and colour features which could possibly exert powerful influences on the decay process. Secondly, exogenous causes such as meals, exercise, stimulants and natural circadian rhythms were thought likely to be sources of influence on the strength of the A/E. To check on these a detailed log was kept of the subjects activities in the hope of indicating the effect of environmental factors. However, this analysis was inconclusive and is not included in this report.

The procedure was altered prior to commencement of the experiments reported in the main results section (Chapter 4). Subjects remained in the experimental room for the entire hour following the period of exposure and were encouraged to read during the inter-test periods. Illumination was constant throughout and from session to session, the subject remaining seated in the same part of the room. Measurements of A/E strength were made at accurately monitored intervals for up to 60 minutes from the end of exposure or until the effect had completely decayed if this occurred in less time. This procedure ensured constant environmental conditions in the post-exposure period, and a uniform testing procedure. The number of readings of A/E strength was standardised at six and these were made at 1, 5, 10, 20, 40 and 60 minutes after the end of exposure. On average, this procedure reduced the number of data points by three when compared with the average number from the exploratory experiments. In addition, this procedure enabled a greater number of experiments to be carried out by one subject (K.B.) who thus undertook the entire programme. For subject K.B., any residual A/E was abolished at the end of each session by a short period of exposure to the opposite pairing of colour and orientation. Total abolition was determined from visual inspection of the test card. 24 hours or longer was allowed to elapse before further experimentation. This procedure did involve certain difficulties and dangers, particularly with respect to hysteresis, which are dealt with in Appendix D of this thesis.

2.5 Subjects

All subjects were adult students or staff at the University of Keele. Prior to participation in the experiments they were screened for colour vision abnormalities by means of Ishihara plates, and visual acuity was checked using a standard test chart. All were naive initially, but the general nature of the phenomenon was explained at some stage. However, subjects were kept naive regarding the purpose of any particular series of experiments and the expectations of the experimenter. An attempt was made to use the same subject for experiments forming part of a series.

2.6 Analysis of temporal parameters



The temporal parameters, and the terminology to be used, may be clarified at this stage:

- 'ON' - The short period of exposure to a grating of particular orientation and colour
- 'OFF' - the short period of darkness separating the discrete exposure periods
- 'CYCLE' - the time elapsing between one onset of a coloured pattern and the next onset of the same coloured pattern
- 'DURATION' - the total time for which a particular cycle is repeated.

CHAPTER 3: EXPLORATORY EXPERIMENTS

3.1 Introduction

The starting point for the main part of this research project was a report by MacKay and MacKay (1973 b). As a result of introducing a quantitative technique for measuring the strength of the after-effect (A/E), these authors were able to describe the time-course of the McCollough Effect. They reported that the strength of the A/E decays rapidly at first and then more slowly, sometimes taking several days to die away completely. When the log. of the strength is plotted against the log. of the time since end of exposure, the data for all ten of their subjects was well fitted by a straight line with a slope of about -0.33.

MacKay and MacKay (personal communication) typically used a stimulation sequence of 6 sec. 'ON'/3 sec. 'OFF' for 10 or 20 minutes. The question underlying the experiments to be reported here is this: Do the characteristics of the stimulation sequence affect the strength or decay rate of the A/E? If there is a total period of adaptation of say 10 min., does it matter how that time is broken up into periods of coloured pattern stimulation and periods of total darkness? One brief report by Hajos (1968) intimated that for certain 'ON' periods (1 or 2 sec.), increasing the 'OFF' was associated with stronger A/E.

Exploratory experiments were conducted early in 1974 to establish whether manipulation of these temporal parameters was associated with changes in either the strength or decay rate, and whether such changes - if they occurred - would be likely to yield any insights into the mechanism underlying the effect. The initial timing values chosen were related to those used by MacKay and MacKay - 6 sec. 'ON'/3 sec. 'OFF', 6 sec. 'ON'/0 sec. 'OFF', 6 sec. 'ON'/6 sec. 'OFF', 3 sec. 'ON'/3 sec. 'OFF', for a constant adaptation duration of 10 min. There were no obvious features to suggest that a straight line on log-log co-ordinates was not the best fit to the data points. There were small differences in the strength and the slope of the line between conditions, but nothing which could not be taken as random scatter.

However, when timing values were chosen which had more extreme 'ON' and 'OFF' periods - 10 sec. 'ON'/1 sec. 'OFF' and 1 sec. 'ON'/10 sec. 'OFF' - a different picture emerged. For the latter sequence the strength was smaller than any previously obtained, but more surprisingly the slope of the decay line seemed to be much steeper. This feature seemed to be confirmed by subsequent experiments, and raised the question whether certain sequences may be associated with a steeper slope of the decay line.

I therefore came to the conclusion that the best policy would be to carry out a correlation and regression analysis of the results of each experiment. This would provide me with the following information: (1) the degree of correlation between log. time and log. strength, which would be a guide to whether or not the data points are well fitted by a straight line, (2) the best estimate for the slope of the line, which would prevent any subjective bias or uncertainty associated with fitting a line by eye, and (3) statistically estimated values for, say, the first and last points, which would indicate any systematic differences between derived and estimated values and so provide further clues as to the shape of the decay plot.

Graphs of data are presented in Appendix F. The line giving the best fit is derived from the regression analysis of the data. It must be emphasised that the general development and direction of the project was determined to a considerable degree by the values so obtained. The results will be presented roughly according to the order in which the experimental questions presented themselves - that is, the order of presentation will show how the project developed rather than attempt a 'logical' analysis of the area.

Towards the end of this phase of the project certain features of the experimental situation were changed, but for convenience of presentation are included here. The experiments carried out after September 1974 used a tachistoscope for presentation of the stimuli. Also included are a number of experiments in which the subject was maintained in conditions of constant illumination during the post-adaptation period, and this allowed a number of comparisons to be made with results previously obtained. These will be referred to at the end of the chapter. The only constant factor throughout this phase of the project was the duration of adaptation, when the question of interest was the effect of timing periods.

3.2 Experimental Results

It soon became apparent that the characteristics of the A/E associated with the 10 sec. 'ON'/1 sec. 'OFF' sequence were different from those associated with a 1 sec. 'ON'/10 sec. 'OFF' sequence, for a constant duration of adaptation (see Fig. F:1, p256). Moreover, with respect to the decay slope for the latter sequence, there are consistent differences from those reported by MacKay and MacKay (1973). A number of things may be clearly seen in Fig. F:1. Firstly, in all cases the initial strength of the A/E associated with the 1 sec. 'ON'/10 sec. 'OFF' sequence is less than that associated with the other sequence. Secondly, the calculated decay slope in the former case tends to be steeper than that associated with the latter. Thirdly, there is some suggestion that for the 1 sec. 'ON'/10 sec. 'OFF' sequence the points are not so well fitted by a straight line on log-log plot.

The smaller strength of A/E associated with the 1 sec.'ON'/10 sec. 'OFF' sequence does not come as too great a surprise, as the subject is exposed to coloured pattern stimulation for a much shorter part of the total adaptation duration. However, it is clear that the strength of the A/E is not related in a simple linear fashion to the factor of the proportion of the adaptation duration for which the subject is exposed to the stimuli. With the short 'ON' period this total duration is about 1 min., while with the longer period this duration is about 9 min. but the strength in the latter case is not nine times greater than that associated with the shorter 'ON' period, as can be seen in Table 3:1.

Table 3:1. The strength of the A/E for two temporal sequences of stimulation

SEQUENCE	TOTAL PAT. STIMULATION	STRENGTH			
		KB	MY	CMJ	SRH
10sec.'ON'/ 1sec.'OFF'	9 min.	2.8	2.4	1.6	2.4
1sec.'ON'/ 10sec.'OFF'	1 min.	1.6	1.1	0.3	0.9
Difference		1.2	1.3	1.3	1.5

The implication would seem to be that the strength of the A/E increases quite rapidly during the first second, and that relatively less is added by lengthening the 'ON'. Moreover, although the absolute values vary, the difference in strength between the two sequences is the same for all subjects - there is a constant increase in the strength for a given increase in the duration of stimulation.

Table 3:11 summarises the findings with respect to the decay slope. For all four subjects the calculated decay slope with the 10 sec. 'ON'/

Table 3:11. Decay slope for two temporal sequences of stimulation

SEQUENCE	DECAY SLOPE			
	KB	MY	CMJ	SRH
10sec. 'ON'/ 1sec. 'OFF'	-0.25	-0.18	-0.18	-0.34
1sec. 'ON'/ 10sec. 'OFF'	-0.35	-0.47	-0.34	-0.67

1 sec. 'OFF' is less steep than that for the other sequence. There is only one occasion on which the calculated decay slope for the 10 sec. 'ON'/ 1 sec. 'OFF' sequence falls within the range of values derived for the other two sequences (subject KB result for 7.6.74.).

The final points to be made concerning these results are related to the question of the goodness of fit of a straight line. The results for the 1 sec. 'ON'/10 sec. 'OFF' sequence for two of the subjects (CMJ and SRH, Fig. F:1) are not so well fitted by a straight line. Moreover, even for the 10 sec. 'ON'/1 sec. 'OFF' sequence, there would seem to be a "drooping" of the data points at very long time intervals after the end of the adaptation period.

The question now arises as to how we may account for the difference in slope between the two sequences. The most obvious possibility is that there is a relationship between the initial strength of the A/E and the rate of decay, weaker A/E being associated with a steeper decay slope.

MacKay and MacKay (1973 b) had commented that briefer exposure (and therefore presumably weaker A/E) yield a lower line of the same slope, indicating that the two aspects of the A/E are not related. However, they had not carried out a systematic investigation of this phenomenon (personal communication).

The question of the possible relationship between the initial strength of the A/E and the decay slope can be investigated quite simply by using the 1 sec.'ON'/10 sec.'OFF' sequence and 'jacking-up' the initial strength by progressively longer durations of exposure. If there is a correlation between the decay slope and the strength in the way suggested, then one would expect that the slope would get less steep for longer adaptation durations. Conversely, if the strength is reduced by shortening the duration of adaptation, then one would expect the decay slope to get even steeper. The results of this series of experiments are shown in Figs F:11 and F:111 and are summarised in Table 3:111. It can be seen that for this

Table 3:111. 1 sec.'ON'/10 sec.'OFF' sequence for various durations of adaptation

Adaptation Duration	KB		MY		SRH	
	Strength	D.S.	Strength	D.S.	Strength	D.S.
44 sec.	0.4	-0.46				
6 min.	0.9	-0.49				
10 min.	1.7	-0.35	1.1	-0.47	0.9	-0.67
15 min.	2.2	-0.49				
20 min.	2.1	-0.40	2.1	-0.50	0.9	-0.30
50 min.	3.4	-0.49	3.4	-0.63	2.0	-0.53

sequence there is some amount of variability in the results for both the strength and the decay slope from one adaptation duration to the next, although in the main the repeat results for any particular duration are fairly similar. In general it can be said that there is no evidence at all for a systematic change in the decay slope with increase in the strength of the A/E. There is some evidence in the results of subject KB and MY of a slightly steeper decay slope associated with the 50 min. adaptation condition. At these long exposures, the results for subjects SRH and MY could be well fitted by a curve.

With respect to the strength of the A/E for different durations of adaptation, it can be seen that the first few minutes have a greater influence, and that the increase is relatively smaller as the adaptation duration gets progressively longer. A similar point was made earlier with respect to the relative influence of the short 'ON' period compared with the long 'ON'.

These experiments failed to show any systematic change in the slope of the decay line correlated with changes in the strength of the A/E for this sequence of stimulation. As further support for the idea that the strength and decay rate are independent functions, Fig. F:IV shows the results of a parallel series of experiments using a 10 sec.'ON'/1 sec. 'OFF' sequence for progressively shorter periods of time. The question in this case is whether the decay slope will become steeper for relatively weaker A/E. As can be seen from this figure and from the summary of results in Table 3:IV, there is no evidence for such a change. The results for 10 min., 6 min. and 3 min. are all fairly consistent, with the exception of the one 'anomalous' result (steep decay slope and low correlation coefficient). The shallow decay slope for the other two

Table 3:IV. 10 sec.'ON'/1 sec.'OFF' sequence with various durations of adaptation

Adaptation Duration	Subject KB	
	Strength	Decay Slope
10 minutes	2.8	-0.25
6 minutes	2.1	-0.20
3 minutes	1.8	-0.20
90 seconds	0.6	-0.12
45 seconds	0.5	-0.11

durations may simply be related to the difficulty of accurately measuring the strength at such low values. This would seem to be the most likely conclusion in view of the way in which the data points are scattered.

Table 3:V is a summary of the results for the two sequences but for different adaptation durations, and helps to reinforce some points already made. Firstly, although the strengths are comparable (with the

Table 3:V. Comparison of results for two sequences of stimulation

SEQUENCE	DURATION	KB		MY		SRH	
		ST.	D.S.	ST.	D.S.	ST.	D.S.
10sec. 'ON'/ 1sec. 'OFF'	10 min.	2.8	-0.25	2.4	-0.18	2.4	-0.34
1sec. 'ON'/ 10sec. 'OFF'	50 min.	3.4	-0.49	3.4	-0.63	2.0	-0.53

strength for the 1 sec.'ON'/10 sec.'OFF' being the greater for two of the subjects), the decay slopes are clearly different. Secondly, the 1 sec.'ON'/10 sec.'OFF' sequence repeated for 50 minutes gives a total period of exposure to the patterns of about four and a half minutes, which is about half the total duration with the other sequence repeated for 10 minutes. This reinforces the point that one cannot account for the strength of the A/E simply in terms of the proportion of the adaptation duration for which the subject is exposed to pattern stimulation. It looks as if coloured pattern stimulation for half the total duration of adaptation can be at least as effective as stimulation for the whole time.

We may summarise the results of these preliminary experiments as follows. In the first place, the strength of the A/E and the associated decay slope are independent functions. Secondly, different decay slopes seem to be associated with different temporal sequences of stimulation. Thirdly, there is no simple relationship between the strength of the A/E and either the length of the discrete stimulus period or the proportion of the total adaptation duration given over to pattern stimulation. In short, it seems that we can give an affirmative answer to our original question - manipulation of the temporal parameters does make a difference to both the strength and the decay slope of the A/E.

If the decay slope is not correlated with the length of the adaptation duration or initial strength of the A/E, the problem is to determine which of the other temporal variables may exert an influence on the rate of decay. Logically, there are only six possibilities in all: (1) the duration of adaptation, (2) the cycle duration, (3) the ratio of the 'ON' period to the 'OFF' period, (4) the discrete 'ON' period alone, (5) the discrete 'OFF' period alone, and (6) particular combinations of 'ON' and 'OFF' periods. The evidence presented so far would tend to rule out (1).

Number (2) also seems unlikely, since the cycle duration was identical (22 sec.) for the two sequences used previously.

In the experiments reported next, two sequences are compared, one with a ½ sec 'ON'/5 sec 'OFF' sequence and the other with a 5 sec 'ON'/½ sec. 'OFF' sequence. In both cases the adaptation duration was 10 min. These sequences were chosen because although the exact timing values are different from those used previously, the ratio of 'ON' to 'OFF' is the same. If the ratio is an important variable with respect to the exponent of the decay slope, then one would expect the results to be very similar to those just presented. If the results are different, then the way in which they are different from the other two sequences may provide some clues regarding the role of the 'ON' and 'OFF'. The steeper decay slope associated with the 1 sec.'ON'/10 sec.'OFF' sequence may be related to either the short 'ON' or the long 'OFF'. If the 'ON' is the important factor, then further reduction to ½ sec. may be expected to give rise to a steeper rate of decay, whereas if the 'OFF' is the key factor one would expect the decay slope to become less steep if this parameter is shortened. A similar line of argument applies to the shallower slope associated with the 10 sec.'ON'/1 sec.'OFF' sequence. If the 'ON' is the important feature, shortening this period should be associated with a slight steepening of the slope (probably to a value somewhere between those associated with each of the sequences used so far). If it is the short 'OFF' which is correlated with the shallower decay slope then the exponent should be reduced.

The results for these two sequences for two subjects are shown in Fig. F:V and are summarised in Table 3:VI, which also enables comparison with the results for the two previously used sequences.

Table 3:VI. Results for four different temporal sequences of stimulation with identical adaptation durations

Sequence	KB		SRH	
	Strength	D.S.	Strength	D.S.
10sec. 'ON'/ 1sec. 'OFF'	2.8	-0.25	2.4	-0.34
5sec. 'ON'/ ½sec. 'OFF'	4.0	-0.39	2.2	-0.27
1sec. 'ON'/ 10sec. 'OFF'	1.6	-0.35	0.9	-0.67
½sec. 'ON'/ 5sec. 'OFF'	1.2	-0.51	0.8	-0.51

Comparing the 10 sec. 'ON'/1 sec. 'OFF' sequence with the 5 sec. 'ON'/½ sec. 'OFF' sequence, it can be seen that for subject KB strength and decay slopes are clearly different; for subject SRH these differences are less marked and are in the opposite direction to those of KB. Comparing results for the 1 sec. 'ON'/10 sec. 'OFF' sequence with those associated with a ½ sec. 'ON'/5 sec. 'OFF' sequence, strengths are similar for both sequences and subjects; decay slopes are clearly different, but again there is no agreement between subjects. The lack of agreement between subjects makes it difficult to draw conclusions, but these results do suggest that the ratio parameter is not critical. The differences between subjects also makes it difficult to draw conclusions regarding the effect of reducing both the 'ON' and the 'OFF' periods. The results are therefore equivocal regarding the role of these two parameters in influencing the slope of the decay line.

Two further points may be made. The first concerns the shape of the decay plot. For both subjects the results for the ½ sec. 'ON'/5 sec. 'OFF' sequence are not particularly well fitted by a straight line and the shape of the plots are fairly similar. Secondly, for KB the strength of the A/E for the 5 sec. 'ON'/½ sec. 'OFF' sequence is greater than that for the 10 sec. 'ON'/1 sec. 'OFF'. This could be due to random variability or reflect a genuine difference related to these timing values. It is not possible to say which is correct at this stage.

In view of the difference between these results and those discussed previously, it seemed worthwhile to confirm the independence of the calculated decay slope and the initial strength of the A/E. The previously described experimental procedure was repeated for the ½ sec. 'ON'/5 sec. 'OFF' sequence for two subjects and the results for the three adaptation durations used can be seen in Fig. F:VI. The previously reported findings are confirmed, as there is no evidence for any decrease in the slope of the decay line as the A/E strength increases by three fold. Once again, it should be noticed that there is a distinct curve to the data points.

The role of the 'ON' and 'OFF' parameters can be investigated in another way. Earlier, it was argued that the steeper decay slope associated with the 1 sec. 'ON'/10 sec. 'OFF' sequence could be related to the short 'ON' period or the long 'OFF'. This problem was investigated further by holding the 'ON' parameter and then the 'OFF' parameter constant in turn, while systematically varying the other, for a constant duration of adaptation. This procedure obviously involved variation in the cycle duration, but the evidence already available indicated that this parameter is not likely to affect the decay slope. Any variation in the strength is also likely to be independent of the decay slope. The ratio of 'ON' to 'OFF' will also be affected and on present evidence its influence cannot definitely be discounted.

In the first series of experiments, the results of which are shown in

Fig. VII, the 'ON' period was constant at 10 sec. and the 'OFF' period was the independent variable. 'OFF' periods of 1, 5 and 10 sec. were used. It can be seen that there is very little variation in the decay slope as the length of the 'OFF' period is progressively increased until it is equal to the length of the 'ON' period, and equal to the longest 'OFF' period used in the previous experiments. The second finding from these experiments is that there is no change in the initial strength of the A/E even though the total period of exposure to the coloured pattern stimuli is reduced from about 9 min. to 5 min. When the 'ON' period is sufficiently long, variation in the length of the 'OFF' period has no effect on either the decay slope or the initial strength. Put another way, the hypothesis might be that so long as the 'ON' period is equal to or longer than the 'OFF' period there will be no systematic variation in the strength or decay slope associated with changes in the length of the 'OFF'.

It has been shown that the decay slope associated with the 1 sec. 'ON'/ 10 sec. 'OFF' sequence is -0.35 and for the 10 sec. 'ON'/10 sec. 'OFF' sequence it is -0.26. If this difference is related to the length of the 'ON' period and is not simply random scatter, then one would expect there to be a systematic change in the decay slope as the length of the 'ON' period is increased, for a constant 'OFF' period of 10 sec. If there is, the question is whether there will be a progressive change or a sharp point of transition.

The results for this series of experiments can be seen in Fig. F:VIII and are summarised in Table 3:VII. There is some amount of variability in these results, part of which may be related to the difficulty in accurately controlling short exposure durations with the equipment in use at the time. The conclusion from these results is that there does not seem to be any clear change in either the decay slope or the strength

Table 3:VII. Changes in decay slope and strength associated with the length of the 'ON' period

ON (sec.)	Strength	D.S.
1	1.6	-0.35
2	1.5	-0.49
3	2.2	-0.35
5	1.5	-0.34
10	2.8	-0.26

as the 'ON' period was increased from 1 sec. to 5 sec. No further experiments were carried out at this stage because of the introduction of a tachistoscope to control stimulus presentation, so there is still uncertainty as to the point or range of values over which decay slope changes.

One further way to study the role of the discrete 'ON' period is to vary only this parameter, while totally removing the dark interstimulus period. The whole of the adaptation duration is then taken up by coloured pattern stimulation. Variation of the length of the 'ON' period will also affect the cycle duration, but the effect of this parameter has been discounted.

Fig. F:IX shows the results for this series of five experiments which were carried out using a tachistoscope to accurately control the period of presentation of the stimuli. In comparison with the results just discussed, the calculated decay slope associated with 'ON' periods of 1 sec. or less are of about the same value as those characteristic of sequences with much longer 'ON' periods. In fact, the results for the whole series are reasonably similar. It should be noted that for the sequence with 1/10 sec.

'ON' period the initial strength is very similar to that of the 1 sec. 'ON'/10 sec.'OFF' and ½ sec.'ON'/5 sec.'OFF' sequence, but there is no suggestion of the steeper rate of decay characteristic of these sequences. There are two possible interpretations for this difference. The first assumes that there is no correlation between the length of the 'ON' period and the decay slope. The second is that the 'ON' is an important parameter, but changes in the length of the 'ON' will only be associated with variation in the decay slope when the discrete exposure periods are separated by some minimum dark interval. The dark periods are assumed to 'isolate' discrete temporal integration periods. Steeper decay slopes may therefore be observed if the 'ON' period is too short to allow maximum integration. If the 'ON' period is too short, maximum integration may still be achieved if successive exposures follow on in rapid succession.

With respect to the strength of the A/E, some changes can be observed which roughly correlate with changes in the value of the 'ON' period. The strength is much reduced when the 'ON' period is only 1/10 sec. and builds up with longer periods. This build-up levels off with 'ON' periods between ½ and 1 sec. The 'ON' period does seem to have a crucial role in determining the strength of the A/E and the results would tend to suggest that the mechanism involved has an integration period of about a second or so.

The final series of experiments investigated the effect of varying both the 'ON' and the 'OFF' equally and together. Sequences were chosen in which the 'ON' and 'OFF' were of equal duration, the shortest value being ½ sec. and the longest 10 sec. This series of experiments is of interest for a number of reasons. Firstly, the ratio is constant throughout and is therefore relevant to questions regarding the importance of the ratio parameter. Secondly, with respect to the strength, will A/E be weaker than for the corresponding 'ON' periods in the previous series, and will the strength vary in the same manner for 'ON' periods less than 1 sec?

The results, presented in Fig. F:X, show two features of particular interest. Firstly, the strength is reduced when the 'ON' and 'OFF' periods are ½ sec. and increase when the periods are 1 sec. Thereafter there is little change. Moreover, the values are very similar to those in the previous sequence. Secondly, there is some suggestion that for the shorter periods the decay slopes may be slightly steeper, though there is too much scatter to be absolutely sure on this point. The results support the idea that the ratio is not important, and that the strength may vary with the 'ON' period when this is less than 1 sec.

3.3 Summary

Decay Slope

1. Certain sequences are associated with steeper decay slopes than are generally typical for the description of the time course of the effect.
2. This steeper decay slope is independent of the duration of adaptation and the initial strength of the A/E. These effects therefore persist for a shorter time than those for other sequences with a similar strength.
3. The slope of the decay line is probably not related to the cycle duration.
4. The ratio of 'ON' to 'OFF' is probably not very important in determining the slope of the decay line.
5. The evidence to date would tend to implicate the discrete ON interval as being the major parameter which can influence the rate of decay of the A/E.
6. The dark interstimulus 'OFF' period acts simply to isolate one discrete 'ON' period from the next period of exposure. Used in this way, the 'ON' and 'OFF' parameters may reveal something about the integration time course of the mechanism underlying the A/E.
7. There is some evidence that the results for certain sequences are not well fitted by a straight line on log-log co-ordinates.

Strength

1. For any particular sequence, increase in the total period of adaptation is generally associated with increase in the initial strength of the A/E and a lengthening of the time to complete extinction. The exception seems to be sequences which have a short

'ON' period, when initial strength is less reliably correlated with adaptation duration.

2. When the adaptation duration is progressively increased, the strength of the A/E rises rapidly at first and then more slowly for longer durations.
3. The initial strength is not related at all to the cycle duration.
4. The strength is not related in a simple way to the ratio of 'ON' to 'OFF'. Again, the strength seems to increase more rapidly in the first few seconds and then less so as the proportion of exposure time increases. Increasing the ratio of ON to OFF above 1:1 seems to have very little systematic effect on the strength.
5. The discrete 'ON' interval alone seems to have quite a substantial influence. Strength increases as 'ON' is increased to roughly 1 sec. but varies very little for values beyond this. This may indicate a critical integration period of 1 sec. or so.

3.4 Statistical Analysis of Data

The reasons for plotting the data on log-log co-ordinates and for carrying out a statistical analysis have already been discussed. Two facts emerged from the results which seemed to require that the data be re-analysed taking the log. of the time values only. These facts were:-

1. Towards the end of 1974 a paper appeared which presented further data regarding the time course of the A/E. Riggs, White and Eimas (1974) claim that on log-log plot their data were not well fitted by a straight line over the entire course of the decay. Rather, the middle course was reasonably well fitted on log-log co-ordinates, particularly for A/E which had a relatively high initial strength. Over the entire course they thought that a better fit to a straight line was obtained on linear-log co-ordinates. They preferred not to speculate on complex forms of equations to handle all their data.
2. There is a distinct curve to the data plot for a number of the results presented here, particularly those associated with a temporal sequence having a short 'ON' and long 'OFF' period. Moreover, for many of the results there is a slight curve to the earlier points.

There were two questions in mind at the time of re-analysis. Firstly, are there systematic variations from a straight line on log-log plot over parts or the entire length of the curve? Secondly, might a better fit for some or all of the data be obtained on linear-log co-ordinates (as suggested by Riggs, White and Eimas)? It was thought that a statistical re-analysis would help answer these questions. The statistics for both forms of analysis are presented at the end of Appendix F. (For the linear-log analysis, the log. is taken of the time values). The main conclusions are summarised in relation to the correlation values and estimated strength at the beginning and end of the post-adaptation period.

3.4.1 Comparison of the correlation values for two forms of analysis

It was originally thought that the correlation values would be a good indication of the goodness-of-fit of the data points to a straight line and would indicate any significant deviations. In the main the correlation values are high, the average value being about -0.95. The values are very similar for the two forms of analysis. There are slightly more occasions when the linear-log analysis produces a higher correlation value - 26 results have a higher value on log-log analysis, 35 are higher on linear-log and 8 results have the same value for both. There do not seem to be any systematic trends, except that certain sequences with a short 'ON' period in particular seem to have higher correlation values from linear-log analysis (e.g. see the results for the series with a 10 sec. 'OFF' period). This analysis raises the possibility that certain sequences may be better fitted on linear-log co-ordinates, but suggest that for the majority of results one form of analysis will be as satisfactory as another.

3.4.2 Estimates of Y1 and YN values derived from a Regression Analysis

A comparison was made of the estimated strength for the first and last data values derived from both forms of analysis, in relation to the figures actually measured. There are two questions. Firstly, which form of analysis tends to give a figure which is nearer to the measured strength. Secondly, are there any systematic trends in the nature of the difference between the values obtained and calculated?

1. Reading at 1 min. after end of exposure.
   (a) There are about twice as many results for which a linear-log analysis provides an estimated value which is nearer to that actually obtained (on 18 occasions a log-log analysis gives a better estimate, on 42 occasions a linear-log is better and for 8 results there is no difference).
   (b) The estimated values from the log-log analysis tend to be higher than the obtained values (48 are higher, 12 are lower and 8 are the same). The linear-log analysis shows the opposite effect, the estimated values being lower than the obtained values (39 are lower, 9 are higher and 20 are the same).
2. The last reading obtained.
   (a) The situation is reversed with the log-log providing an estimated value nearer to that obtained (29 better for log-log, 15 for linear-log and 24 results for which there is no difference.
   (b) A similar picture emerges as for the reading at 1 min. The estimated values tend to be higher for a log-log analysis (32 higher, 8 lower and 28 the same), but lower from a linear-log analysis (39 lower, 11 higher and 18 the same).

3.4.3 Re analysis of results related to the changes in experimental procedure

Towards the end of the period of exploratory experiments it was decided to plot the decay for only a restricted period and to control illumination and environmental conditions during this post-exposure period. The statistics were re-considered with these two changes in mind.

There are two ways in which the data can be analysed. Firstly, for any one particular experimental result it is possible to re-compute the necessary statistical functions but using, say, only the first six readings. The derived values may then be compared with those based on a larger number of data points. Secondly, a number of repeat runs were carried out in which these new conditions were applied. These results can be compared directly with the other experiments using that particular temporal sequence. Reconsidering the results in this way confirms that analysing only six data points does not affect the general conclusions regarding analysis in terms of linear-log or log-log data values and does not introduce any systematic change in calculated decay slopes. Furthermore, the results from the limited number of runs under conditions of controlled post-adaptation illumination are very similar to those lacking this control procedure. The general conclusion is that the altered experimental procedure is not likely to substantially alter the values derived from a statistical analysis of the results.

3.4.4 Summary

1. Correlation values derived from log-log and linear-log data are high. On this basis it is not possible to choose one function in preference to another.
2. There are systematic discrepancies between the measured strength and the estimates calculated from log-log values. Moreover, a number of the plots of results have a distinct curved shape. It therefore seems unlikely that this statistic will be very useful as an indicator of significant changes in the shape of the plot.
3. To allow a consistent approach to the problem of describing the time course of the decay, results will continue to be plotted on log-log

co-ordinates. Graphs of averaged data values will be shown (except where there is only one result for a particular sequence) and error bars will be used to indicate the variability between results. The line giving the best fit will not be shown on the graphs. The decay slopes will continue to be calculated as these will give an indication of any systematic changes in the rate of decay.

4. A number of results are non-linear on a log-log plot. For these results, calculation of an equivalent decay slope from log-log values will allow a consistent approach to the problem of the description of the decay of the A/E. In addition, all results from the parametric study (Chapter 4) were plotted on linear-linear and linear-log co-ordinates and some of the latter will be shown at appropriate points in the text. However, it must be emphasised that the primary interest concerned systematic changes in the rate of decay - no attempt has been made to test the goodness of fit on all possible functions.

5. By the time the A/E has decayed to a low level the subjective appearance is of very desaturated and "patchy" colours on the test card. For subject K.B. this tended to occur when the strength had fallen below a level of approximately 0.5. It was felt that colour matches became very unreliable under these conditions and so it was decided not to plot the decay once it had fallen below this level. This resulted in fewer than six data points for some results. However, it became apparent that this policy would lead to loss of essential information. As the project developed it became necessary to look more carefully at the shape of the plot and to take more frequent readings at later stages of the decay process.

CHAPTER 4: A PARAMETRIC STUDY OF THE EFFECTS OF TEMPORAL PARAMETERS OF STIMULATION ON STRENGTH AND RATE OF DECAY OF THE MCCOLLOUGH EFFECT.

4.1 Introduction

The exploratory experiments reported in the last section established that both the strength of the A/E and the rate of decay for a given total duration of exposure do vary with the temporal sequence employed. The limited evidence accumulated tended to exonerate the cycle time as a critical factor and probably the ON:OFF ratio, and seemed to implicate variation of the 'ON' period as correlating with the changes observed. The dark interstimulus period perhaps functions to isolate the discrete periods of stimulation and as such has a 'negative' role. The idea emerged that there may be a critical time period - of the order of a second or perhaps longer - over which the mechanism underlying the effect integrates the visual input. Variation of the 'ON' within this time period has an important influence on both the strength of the A/E and the rate of decay. The primary reason for continuing this study of the influence of timing parameters was to gather more substantial and reliable evidence regarding the time course of this integration period by establishing the precise contribution of the 'ON', 'OFF' and ratio parameters, for values over the range ¼ sec. to 10 sec. A more thorough study was also made of the effect of adaptation duration on the establishment and subsequent decay of the A/E.

To this end, a tachistoscope was introduced into service which provided more accurate control over the period of stimulation. The post-adaptation environment of the subject was controlled to the greatest extent possible. It was necessary to repeat most of the experiments carried out earlier, since many of these had involved an 'ON' or 'OFF' period which was relatively short and therefore not accurately controlled, and the influence of environmental factors was uncertain. In addition, the standard period of adaptation was increased from 10 to 15 min. in order to perhaps provide greater stability of results - many subjects only build up a fairly weak A/E in 10 min. of adaptation, and weak A/E tend to be "patchy" (A/E colours desaturated and not uniform over the test card). In what follows an adaptation duration of 15 min. may be assumed, unless some other time is actually stated.

Several of the series of experiments were used again and new ones added to follow up the ideas already developed. The rationale underlying the choice of the various series is quite simple and may be outlined briefly. If the 'ON' period is itself the critical factor, then systematic manipulation of this parameter for any given (constant) 'OFF' period should reveal changes in the strength and/or decay slope. Moreover, the changes observed (if any) should be the same whatever the constant 'OFF' value. So for various OFF values (e.g. 10 sec., 5 sec., 1 sec. and 0 sec.) variation of the 'ON' period (from ¼ sec. to 10 sec.) should have the same effects at each of these OFF values. Failure to find this similarity between the different 'OFF' series of experiments must necessarily imply that the 'ON' is not the only important factor. A similar argument applies if the 'OFF' period itself is the crucial parameter. For any particular 'ON' period (10 sec., 5 sec., 1 sec., etc.), variation of the 'OFF' should reveal the changes in the decay slope and/or strength, and these changes should be the same whatever the 'ON' period. Failure to find this similarity between the different series of experiments must imply that the 'OFF' period is not the one single factor underlying whatever changes are observed. Equally, if the ratio of 'ON' to 'OFF' is the critical parameter, for any particular ratio variation in the absolute 'ON' and 'OFF' values should not be associated with any changes in the strength or decay slope. Changes in decay slope and/or strength should correlate with changes in the ON:OFF ratio.

Adaptation duration effects may be investigated by varying this parameter alone, for any given temporal sequence. Repeating this procedure for different temporal sequences will confirm whether or not the effects are independent of the absolute 'ON' and 'OFF' periods. The cycle duration may also have an effect, but this parameter was largely discounted early in the exploratory phase.

As the project progressed, some further questions emerged which led to the introduction of experiments involving new temporal sequences. These questions were as follows:

(1) is there a 'peak' in both strength and decay slope for 'OFF' periods of about 1 sec., whatever the 'ON' period?

(2) is there a general peak at about 5 sec. 'ON'/1 sec. 'OFF'?

(3) do these changes reverse sharply when the 'OFF' period is increased to 2 sec.? and

(4) is the decay rate for certain sequences described better by plotting the data points on linear-log coordinates?

Obviously, there will be 'overlap', in that particular temporal sequences will fall into two or more series of experiments. For purposes of analysis and clarity of presentation, this will necessarily involve some repetition of discussion of the results for particular temporal sequences. The results will therefore be presented under the four broad headings previously outlined: the relationship of decay slope and strength to (1) the 'ON' period, (2) the 'OFF' period, (3) the ratio of ON:OFF and (4) the influence of adaptation duration.

Graphs for the experiments involving changes in 'ON' and 'OFF' periods are presented in Appendix G and are organised on successive pages on the basis of the 'ON' period for the experiment - that is, each page will show the results for a particular 'ON' period for the various 'OFF' periods associated with that 'ON', while successive pages will show the results for progressively longer 'ON' periods. This will obviate the need for repetition of graphs of any particular temporal sequence. Graphs for experiments involving variation in duration are presented in Appendix H.

4.2 Experiments in which the 'ON' period is the independent variable, for a number of constant 'OFF' periods

The exploratory experiments showed that when the 'ON' period is lengthened, strength increases for 'OFF' periods of 10 sec. and 0 sec., but the range of 'ON' periods over which the change takes place is different for the two 'OFF' periods. Moreover, shorter 'ON' periods are associated with a steeper decay slope for the 10 sec. 'OFF' series, which is not the case for the 0 sec. 'OFF' experiments. The results are clearly different for the two series. The purpose of the next experiments to be reported was to define more precisely the time course of these changes.

4.2.1 'ON' period varied, for a constant 'OFF' period of 10 sec.

(a) Strength of A/E

For two of the subjects the shortest 'ON' period used was ½ sec. but for the other two it was 1 sec. For all four subjects the strength is about 1.0 when the 'ON' period is 1 sec. (see Fig. 4.1). For subject K.B. the strength is about 0.5 at ½ sec. perhaps indicating a linear, rapid rise in strength for 'ON' periods up to 1 sec., or a strength of

FIG. 4.1(a)

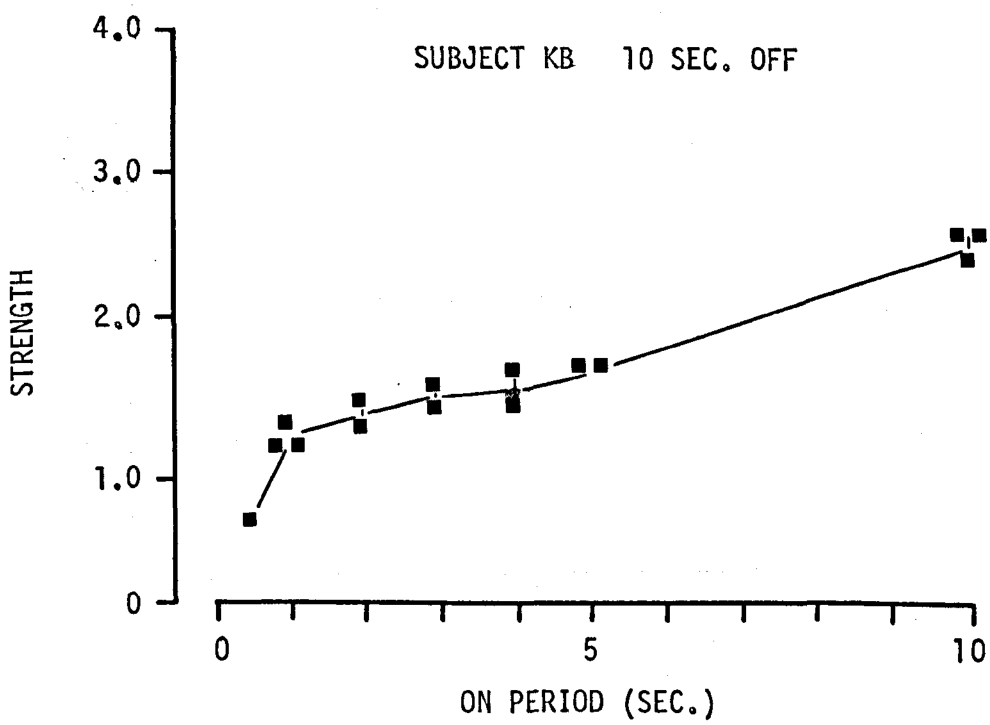


FIG. 4.2(a)

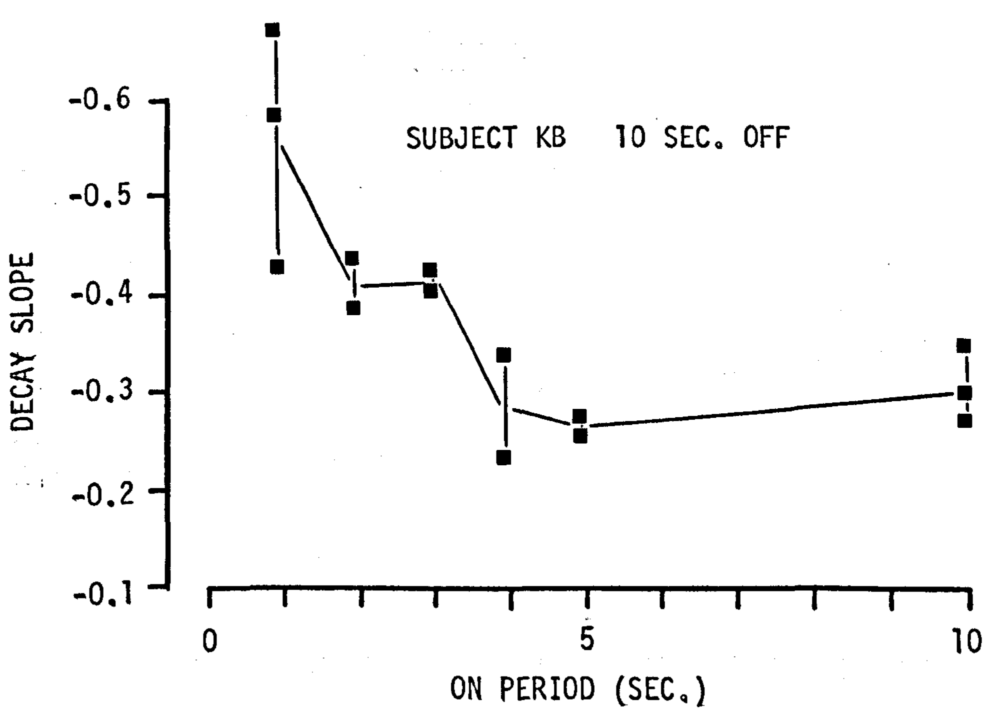


FIG. 4.1 (b)

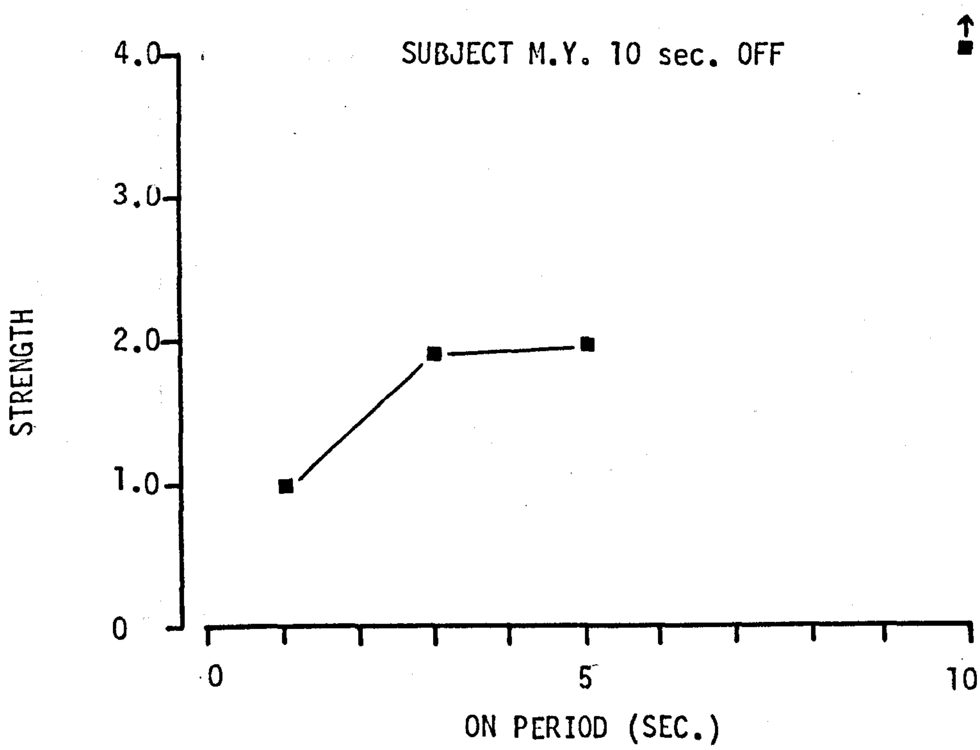
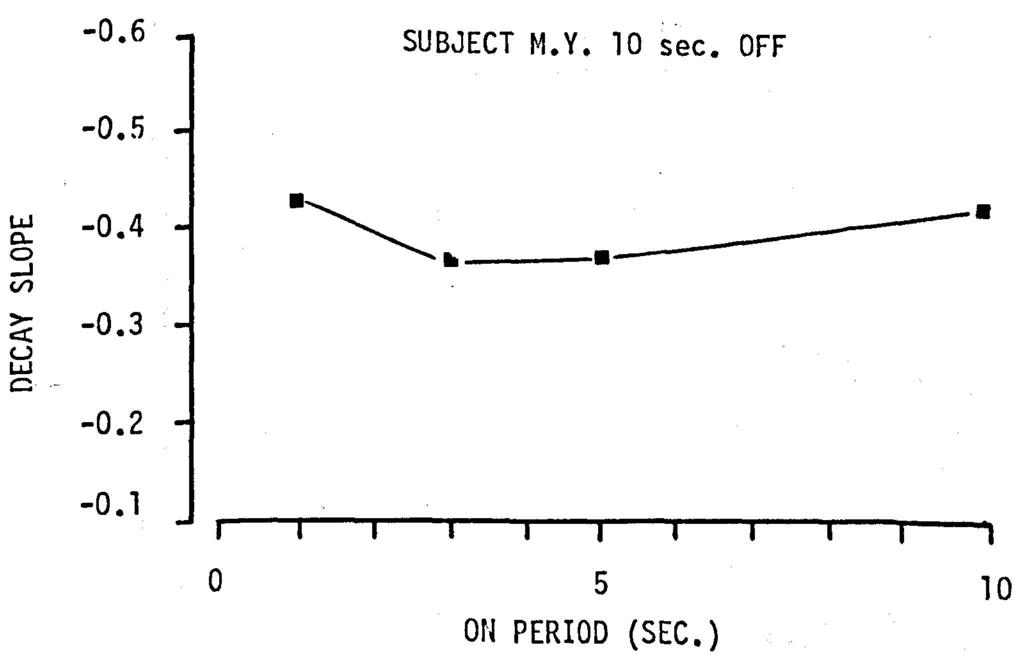
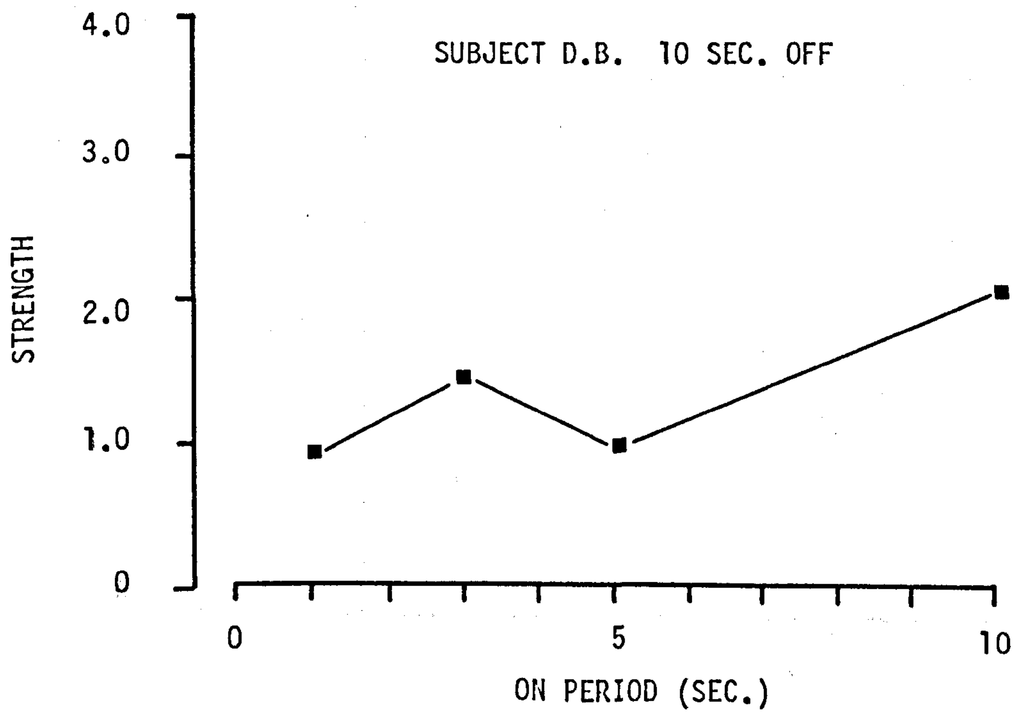


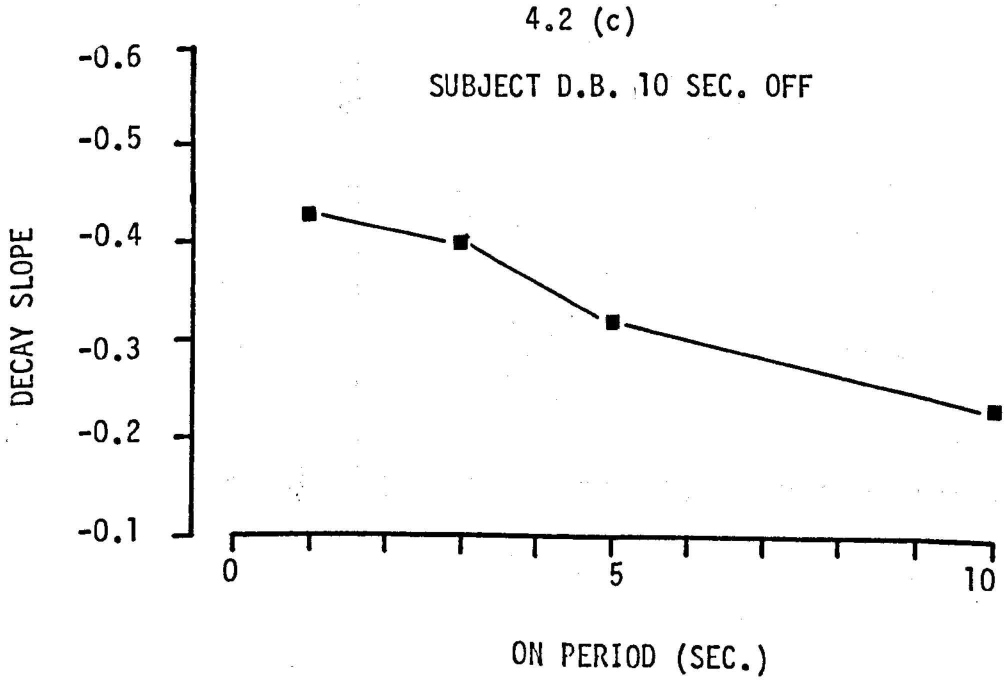
FIG. 4.2 (b)



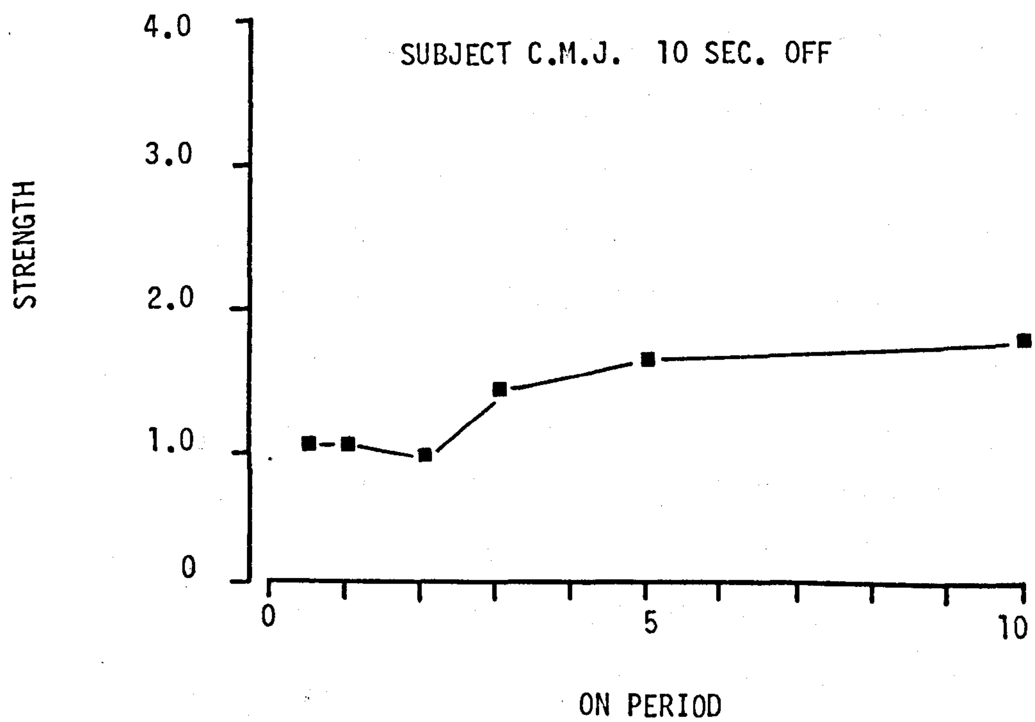
4.1 (c)


SUBJECT D.B. 10 SEC. OFF
4.0
3.0
2.0
1.0
0
STRENGTH
0
5
10
ON PERIOD (SEC.)

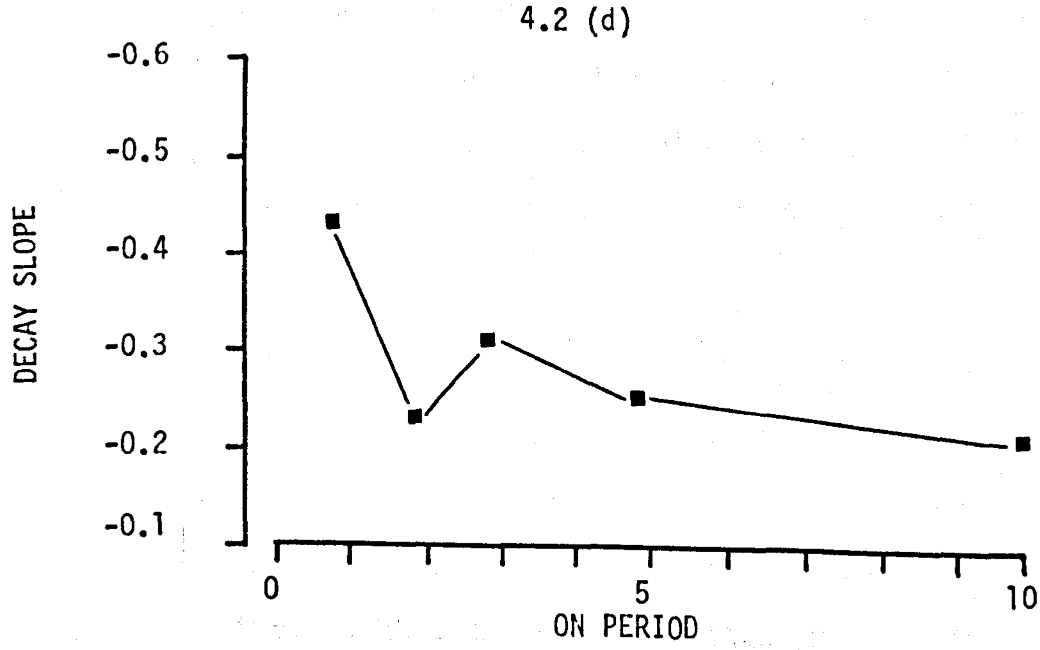
4.2 (c)


SUBJECT D.B. 10 SEC. OFF
-0.6
-0.5
-0.4
-0.3
-0.2
-0.1
DECAY SLOPE
0
5
10
ON PERIOD (SEC.)

4.1 (d)


4.0
3.0
2.0
1.0
0
STRENGTH
SUBJECT C.M.J. 10 SEC. OFF
0
5
10
ON PERIOD

4.2 (d)


-0.6
-0.5
-0.4
-0.3
-0.2
-0.1
DECAY SLOPE
0
5
10
ON PERIOD

1.0. 'ON' periods from 1 sec. to 10 sec. are associated with a steady, almost linear rise but with a much shallower slope, though there is some suggestion of a "levelling-off" between 3 and 4 sec. However, for subject C.M.J. the strength is about 1.0 at ½ sec. and does not change much up to 'ON' periods of 2 sec. 'ON' periods between 2 and 5 sec. are associated with a further shallow rise, after which there is virtually no change. Subject D.B. shows a similar 'plateau' effect, but one which extends over a period from 1 to 5 sec. after which there is again a rise in strength at 10 sec. 'ON'. The results for M.Y. are slightly different in that although there is a rapid rise within the first 3 sec. and a slight plateau between 3 and 5 sec., there is a rapid rise again in the strength beyond 'ON' periods of 5 sec.

Although there are obvious individual differences, looking at the results as a whole a number of generalisations may be made. Firstly, there is a rapid rise in strength to 1.0 which is achieved when the 'ON' period is ½ sec. to 1 sec. in duration. There is then a period of less rapid rise in strength with lengthening of the 'ON' period, the results for some subjects suggesting that there may be a plateau within a restricted part of the range up to 'ON' periods of 5 sec. The evidence is not clear-cut on this point. 'ON' periods greater than 5 sec. are accompanied by a further rise, but the rate varies considerably between subjects.

(b) Decay slope

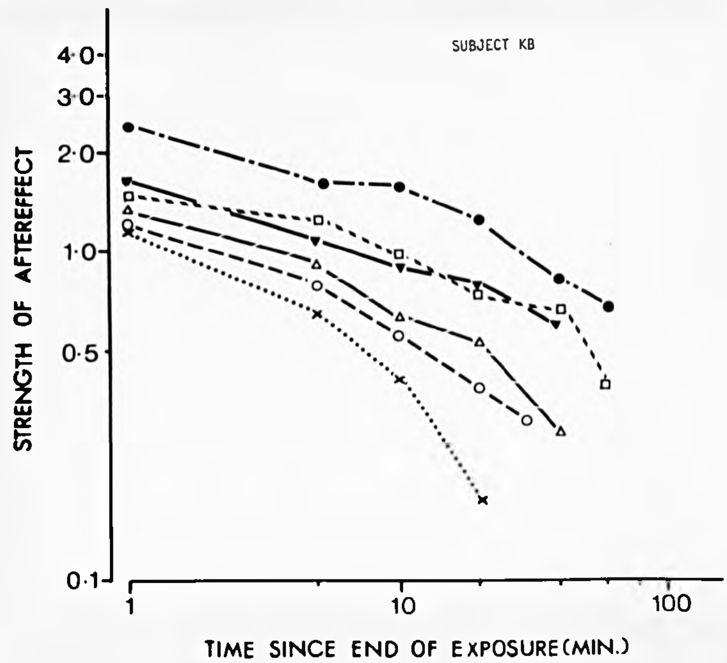
Fig. 4.2 shows a plot of the decay slope against the 'ON' period, the values being derived from a Regression Analysis in which the log. is taken of both time and strength. No attempt was made to derive a decay slope for the experiment with ½ sec. 'ON' since the initial strength was small and would have decayed to about 0.1 or less within 5 min. (see also results for sequence 1 sec. 'ON'/5 sec. 'OFF'). It can be seen for subject K.B. that for an 'ON' period of 1 sec. the decay slope is steep, though there is some overlap of the lower data points with those for 'ON' periods of 2 and 3 sec.. The results are very similar at 2 and 3 sec. 'ON' but then there is a clear drop between 3 and 4 sec. after which there is very little change. The results for the other three subjects all show higher decay slopes at 1 sec. than for any other 'ON' period but beyond that the characteristics are different. For two of the subjects there is an overall decline as the 'ON' period is increased from 1 to 5 sec. after which there is very little change. The results for M.Y. show no clear change in the decay slope.

Examination of the graphs in Appendix G shows that many of the results, especially when the 'ON' period is less than about 3 secs., are not fitted very well by a straight line on log-log plot. Fig. 4.3 summarises these results for each subject. All the results for each subject for the series of six experiments are presented on one graph, ignoring the scatter about each point to allow the overall trend to be seen more clearly. The results are presented on log-log and on linear-log plot. A clear sequence of changes can be seen in the results of subject K.B., for whom there are more data. On a log-log plot, the decay is clearly non-linear when the 'ON' period is 1 sec., but becomes more nearly linear as the 'ON' period is increased to 2 and 3 sec. There is very little deviation from linearity for 'ON' periods of 4, 5 and 10 sec. However, on linear-log plot the results for the 1, 2 and 3 sec. 'ON' periods could be fairly well fitted by straight lines of constant slope. The results for the 4 sec. 'ON' period would also perhaps be slightly better fitted by a straight line on linear-log coordinates. There is nothing to choose between the two plots in describing the results for 5

FIG. 4.3 10 SEC. OFF

×	1 SEC. ON
○	2 SEC. ON
△	3 SEC. ON
□	4 SEC. ON
▼	5 SEC. ON
●	10 SEC. ON

FIG. 4.3 (a)


SUBJECT KB
4·0
3·0
2·0
1·0
0·5
0·1
STRENGTH OF AFTEREFFECT
1
10
100
TIME SINCE END OF EXPOSURE(MIN.)

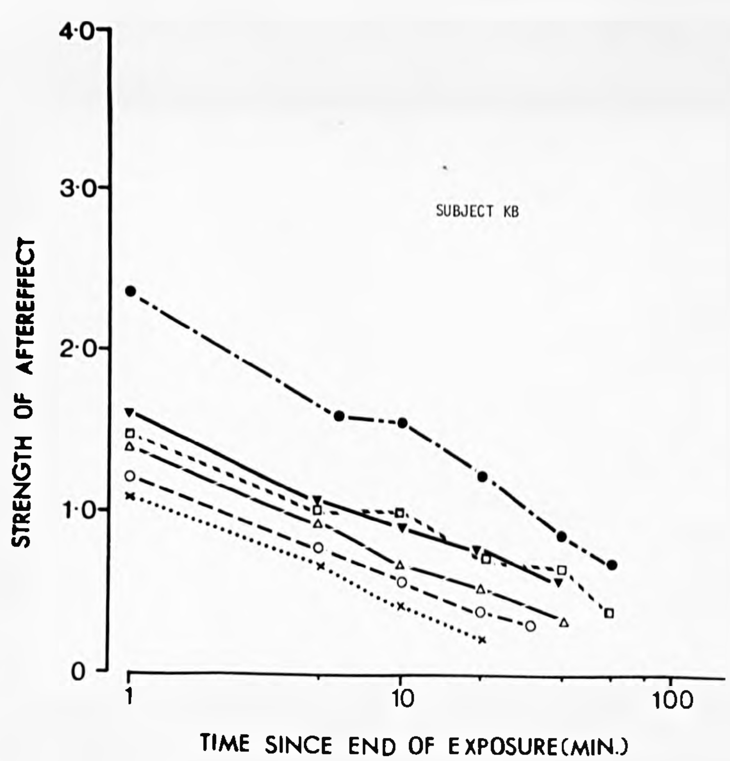
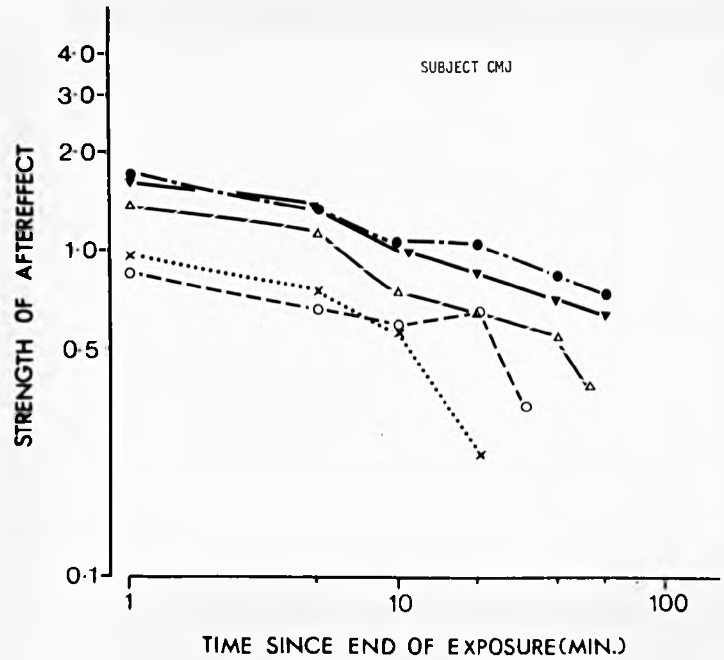

SUBJECT KB
4·0
3·0
2·0
1·0
0
STRENGTH OF AFTEREFFECT
1
10
100
TIME SINCE END OF EXPOSURE(MIN.)

FIG. 4.3 (b)


SUBJECT CMJ
4·0
3·0
2·0
1·0
0·5
0·1
STRENGTH OF AFTEREFFECT
1
10
100
TIME SINCE END OF EXPOSURE(MIN.)

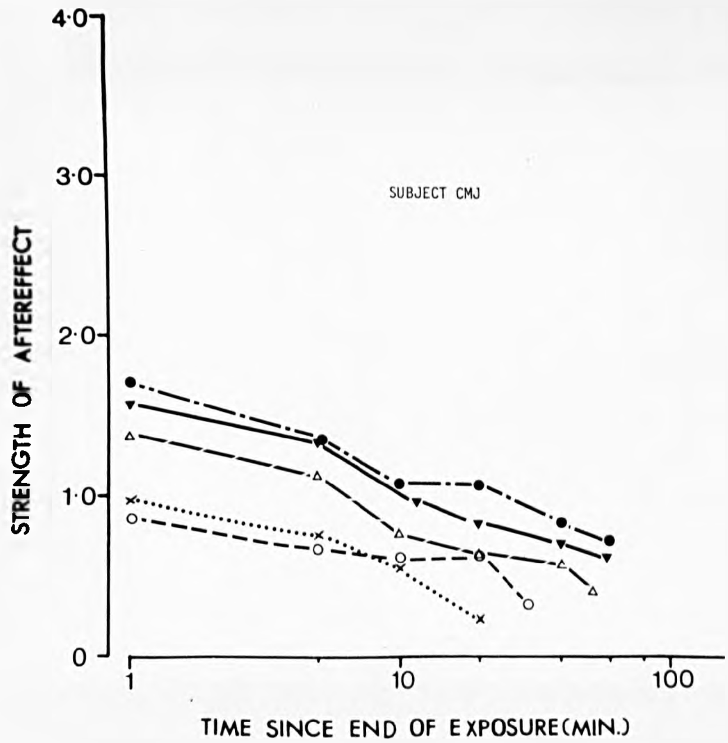
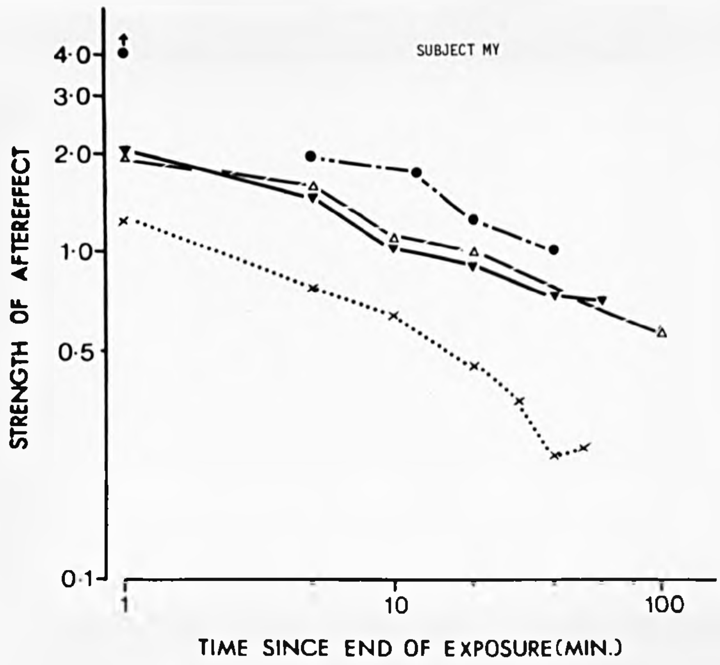

SUBJECT CMJ
4·0
3·0
2·0
1·0
0
STRENGTH OF AFTEREFFECT
1
10
100
TIME SINCE END OF EXPOSURE(MIN.)

FIG. 4.3 (c)


SUBJECT MY
STRENGTH OF AFTEREFFECT
4·0
3·0
2·0
1·0
0·5
0·1
1
10
100
TIME SINCE END OF EXPOSURE(MIN.)

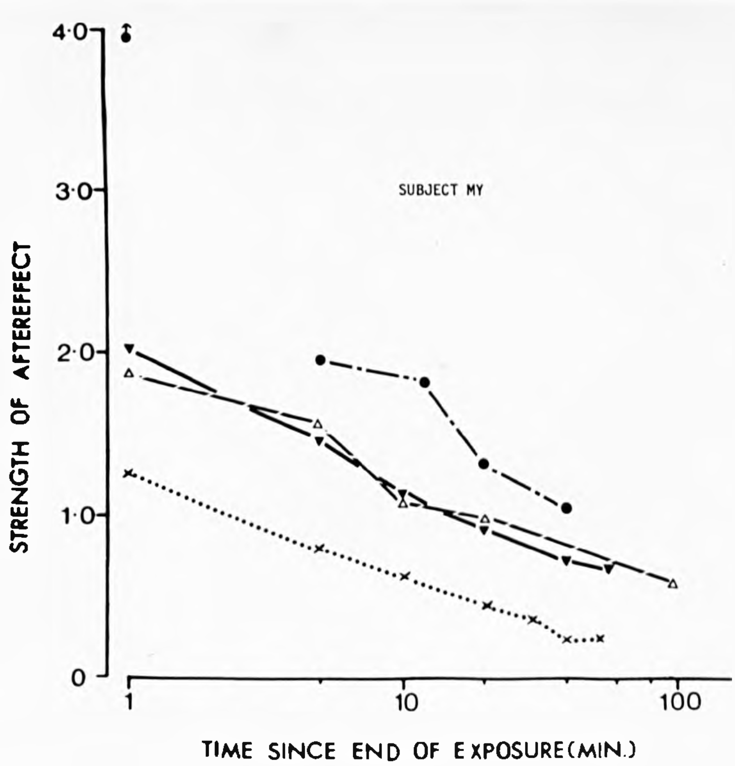
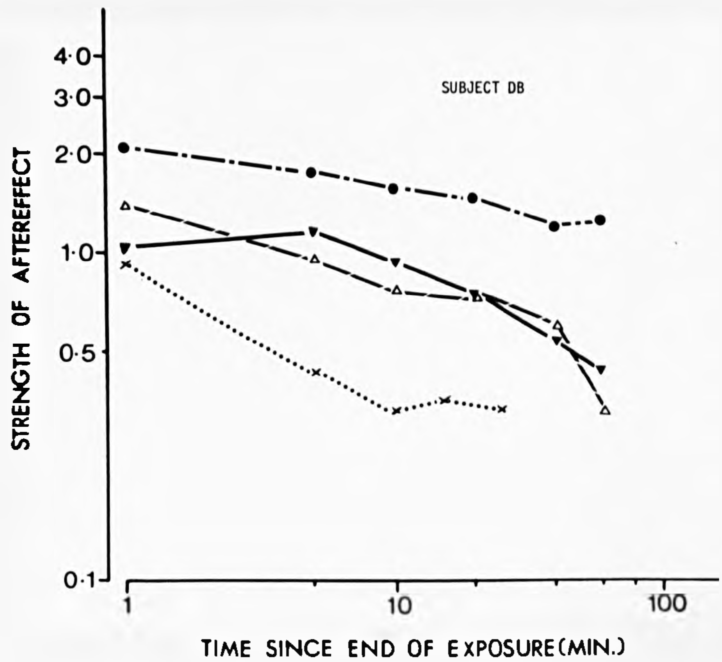
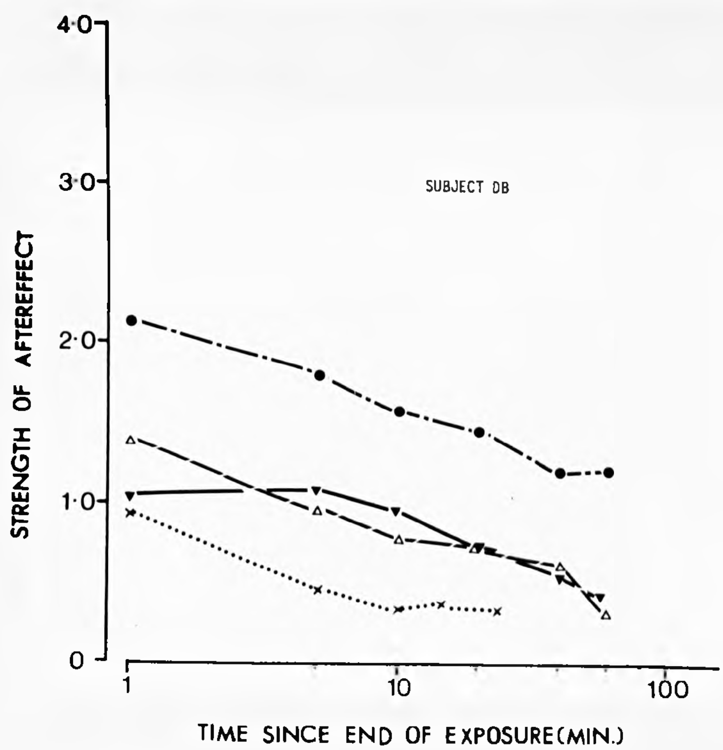

SUBJECT MY
STRENGTH OF AFTEREFFECT
4·0
3·0
2·0
1·0
0
1
10
100
TIME SINCE END OF EXPOSURE(MIN.)

FIG. 4.3 (d)


SUBJECT DB
STRENGTH OF AFTEREFFECT
4·0
3·0
2·0
1·0
0·5
0·1
1
10
100
TIME SINCE END OF EXPOSURE(MIN.)


SUBJECT DB
STRENGTH OF AFTEREFFECT
4·0
3·0
2·0
1·0
0
1
10
100
TIME SINCE END OF EXPOSURE(MIN.)

sec. and 10 sec. 'ON' periods.

The results for subject C.M.J. are very similar to those of K.B. The two graphs of results for M.Y. show a similar effect for the 1 sec. 'ON' period, but for the 3, 5 and 10 sec. 'ON' periods the results could be equally well fitted by a straight line on either co-ordinates. For subject D.B. there is not much to choose between the plots on either pair of co-ordinates. There is no clear change over the range 1 sec. to 5 sec. 'ON', though the data show a much better fit to a straight line on log-log axes for 10 sec. 'ON'.

At this stage it is difficult to draw any firm conclusions regarding the non-linearity of decay on log-log plot associated with the shortest 'ON' periods. This feature could be of some theoretical interest or may simply relate to a subjective threshold level. The time course of transition to a linear decay on log-log co-ordinates is difficult to determine precisely and may vary between subjects, but is within the range of 'ON' periods from 2 sec. to 5 sec.

4.2.2 <u>'ON' period varied for a constant 'OFF' period of 5 sec.</u>

(a) Strength of A/E

Fig. 4.4 summarises the results for this series of experiments. The results for subject K.B. show several of the features evident in the graph of the results for the previously discussed series of experiments. The build-up in strength is most rapid in the first two seconds rather than only the first second and then plateaus between 2 and 5 sec. The strength at 5 sec. 'ON' in this sequence is very similar to that for the 10 sec. 'ON' period when the 'OFF' is 10 sec. It is at this point that the 'ON' and 'OFF' periods are of equal duration. In the present series, there is no further change in the strength when the 'ON' period is increased from 5 to 10 sec. though in the previous series the strength continued to rise with a similar increase in the length of the 'ON' period.

The results for the other subject are not identical with those for K.B. The strength for ½ sec. and 1 sec. 'ON' periods are very similar, but at 2 sec. 'ON' the strength drops down again, and is followed by a very sharp rise at 5 sec. 'ON'. Unfortunately, it was not possible to complete this series of experiments on this subject.

Table 4.2 makes some comparisons between the results for the two sequences for subject K.B., who was the only subject to take part in both.

Table 4.2. Comparison of strength for two series of experiments

	ON sec.	OFF sec.	Strength
ON = 1/10 OFF	½ 1	5 10	0.6 1.0
ON = 1/5 OFF	1 2	5 10	1.3 1.2
ON = 2/5 OFF	2 4	5 10	1.8 1.4
ON = OFF	5 10	5 10	2.1 2.4

The ratio of ON:OFF would clearly seem to be important, since different 'ON' and 'OFF' periods are associated with similar strength. This is the case at least up to the point when the ON = OFF. This is in agreement with the suggestion made on the basis of the exploratory experiments.

FIG. 4.4(a)

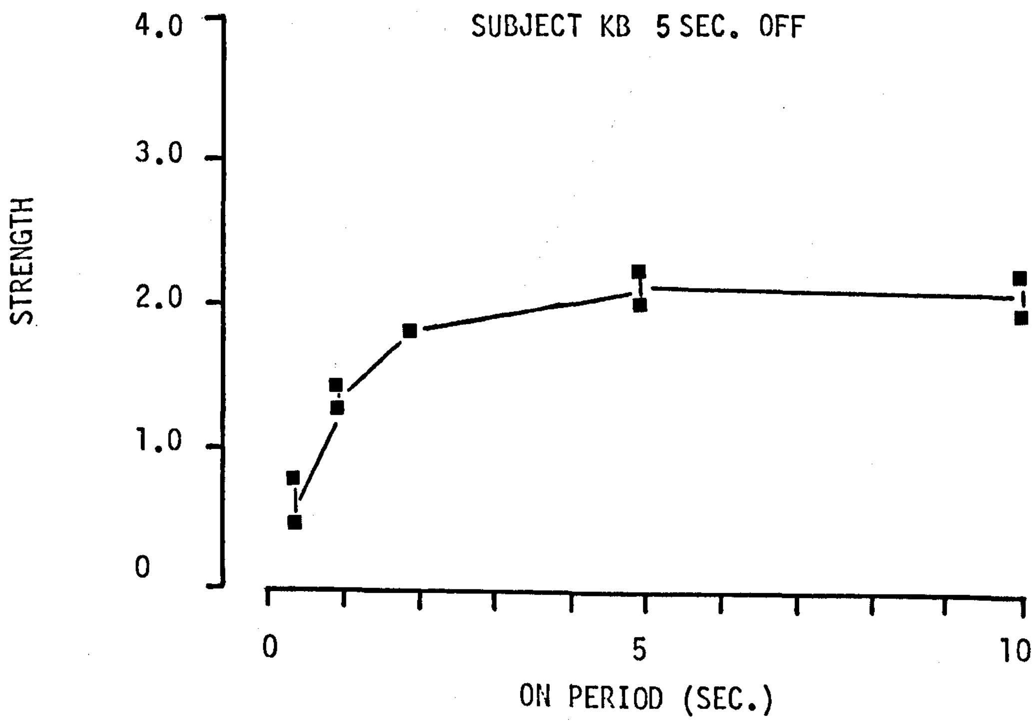


FIG. 4.5

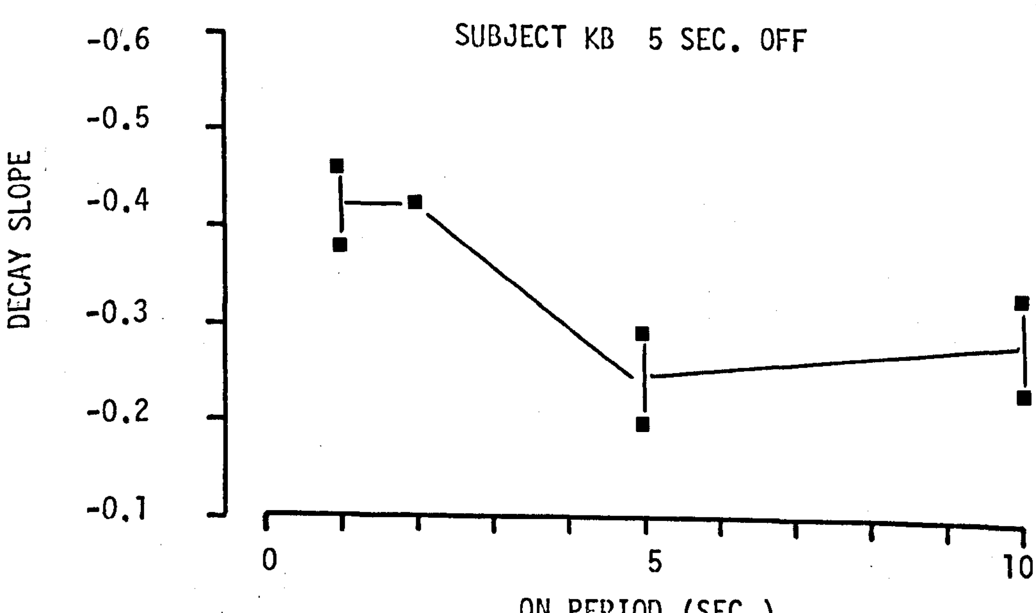
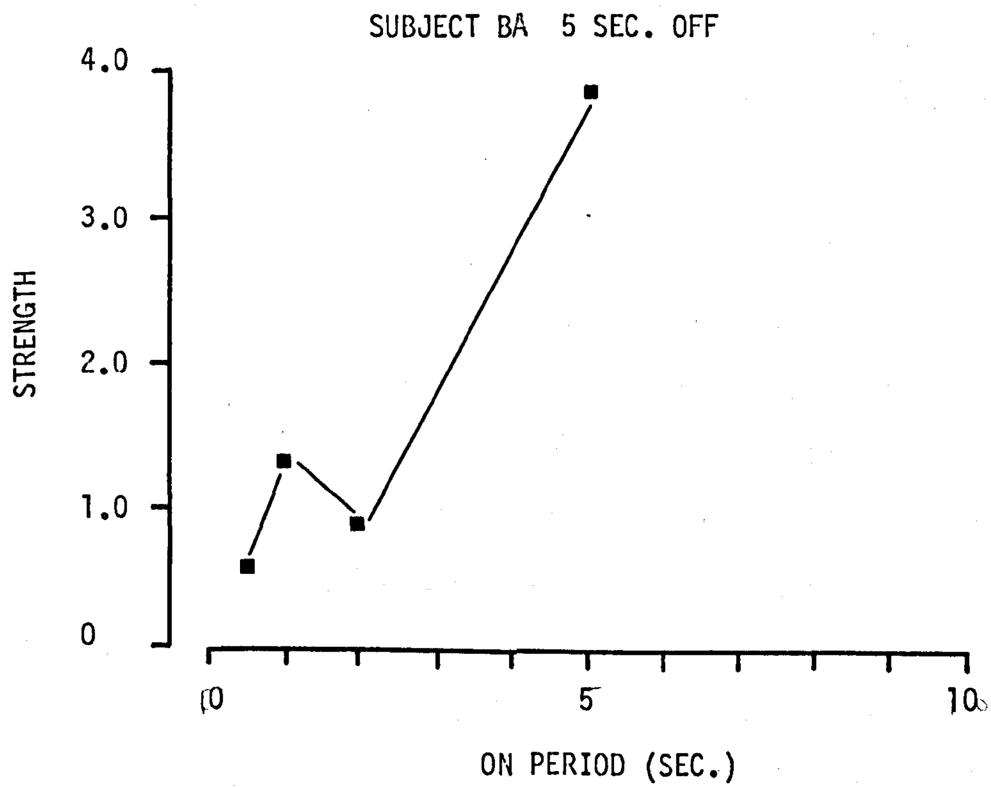


FIG. 4.4(b)



However, the fact that the strength at ½ and 1 sec. 'ON' is very similar for the two sequences and for all subjects, combined with the fact that in the main the rate of increase is greater within the first second or so, may perhaps indicate that stimulation periods of about 1 sec. are themselves also critical.

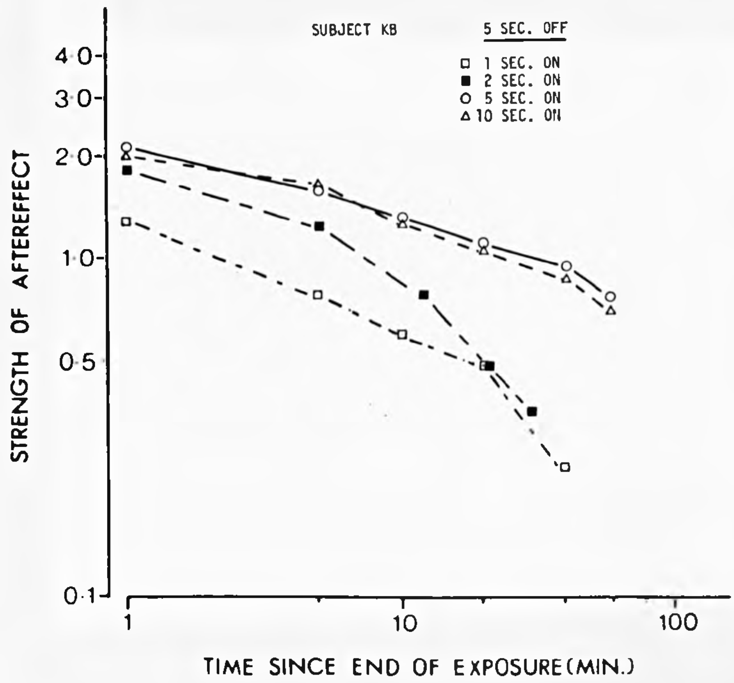
(b) Decay Slope

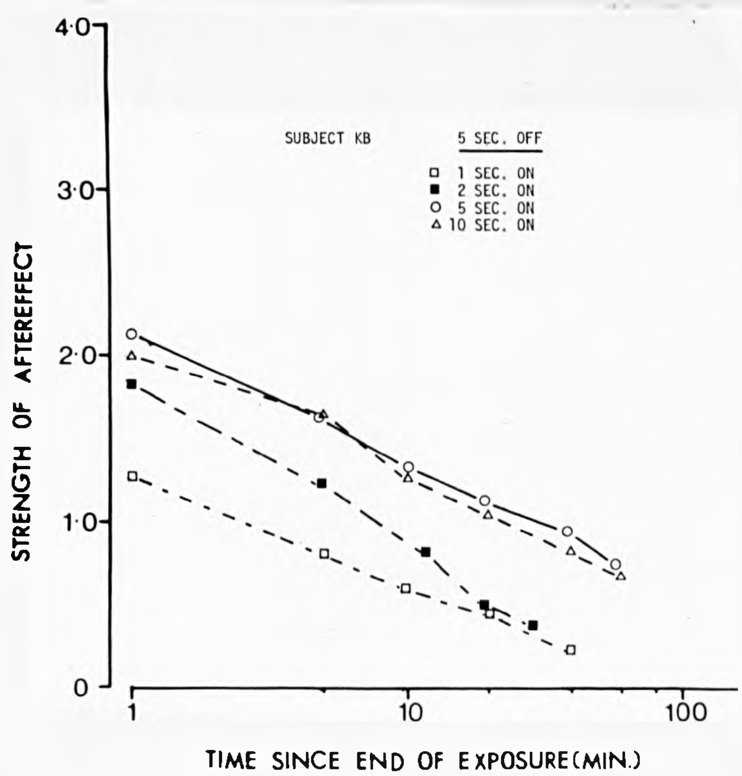
Fig. 4.5 shows the relationship between the decay slope and the length of the 'ON' period when the 'OFF' period in all cases is 5 sec. The estimate for the decay slope is derived from analysis in which the log. is taken of the time and the strength. Owing to pressure of time, it was unfortunately not possible to follow the decay of the A/E for the other subject who took part in this series of experiments.

The calculated decay slopes for 1 sec. and 2 sec. 'ON' periods are approximately -0.4, which drops to -0.25 when the 'ON' period is 5 sec. and is about the same for the 10 sec. period. These results are very similar to those for the same subject for the series of experiments with a 10 sec. 'OFF' period, indicating that there is a change in the decay slope somewhere within the range of 'ON' periods between 2 and 5 sec. It is unfortunate that time did not permit completion of this series - it would be of importance to determine whether there is again a sharply defined point of transition for 'ON' periods between 3 and 4 sec.

The graphs for these experiments, presented in Appendix G, show that for 1 and 2 sec. 'ON' there is a "drooping" of the data points on log-log co-ordinates. Fig. 4.6 is a graphical summary, on log-log and linear-log co-ordinates, of the series of experiments. Scatter bars are omitted for clarity. For the two sequences with the shorter 'ON' periods, there is quite clearly a better fit to a straight line on

FIG. 4.6


SUBJECT KB
5 SEC. OFF
1 SEC. ON
2 SEC. ON
5 SEC. ON
10 SEC. ON
STRENGTH OF AFTEREFFECT
4·0
3·0
2·0
1·0
0·5
0·1
1
10
100
TIME SINCE END OF EXPOSURE(MIN.)


SUBJECT KB
5 SEC. OFF
1 SEC. ON
2 SEC. ON
5 SEC. ON
10 SEC. ON
STRENGTH OF AFTEREFFECT
4·0
3·0
2·0
1·0
0
1
10
100
TIME SINCE END OF EXPOSURE(MIN.)

linear-log co-ordinates. For the 5 and 10 sec. 'ON' periods the results are perhaps slightly better fitted on log-log co-ordinates.

4.2.3 <u>'ON' period varied, for a constant 'OFF' period of 1 sec.</u>

(a) Strength of A/E

Only one subject took part in the whole series of experiments, and the scatter plot of strength against 'ON' period is shown in Fig. 4.7. The first point of note is the rapid rise in strength. With a ½ sec. 'ON' period the initial strength has already reached 1.0 and increasing the 'ON' period to 1 sec. is associated with an increase in strength to a mean value of 2.8. This rapid rise for 'ON' periods up to 1 sec. is similar to the results for the two sequences previously discussed, though the rate of increase is much greater. Shortening the 'OFF' has in each case been associated with an increased rate of rise in the strength correlated with lengthening the 'ON' period.

Lengthening the 'ON' period beyond 1 sec. is associated with further changes in mean strength, but there are two features which suggest that these may not be significant. Firstly, the direction of change is not constant, strength increasing and then decreasing for progressively longer 'ON' periods. Secondly, and more important, there is considerable scatter of data points, which make the mean values unreliable estimates. This degree of scatter is a phemonenon not previously encountered. Indeed, there was good correspondence between repeat results for most of the sequences previously discussed.

The final point concerns the ratio of ON:OFF. For the 5 sec. 'OFF' series of experiments there was no further increase in the strength when the 'ON' period was increased from 5 sec. to 10 sec. or when for the first time the 'ON' period was longer than the 'OFF'. In this present

FIG. 4.7

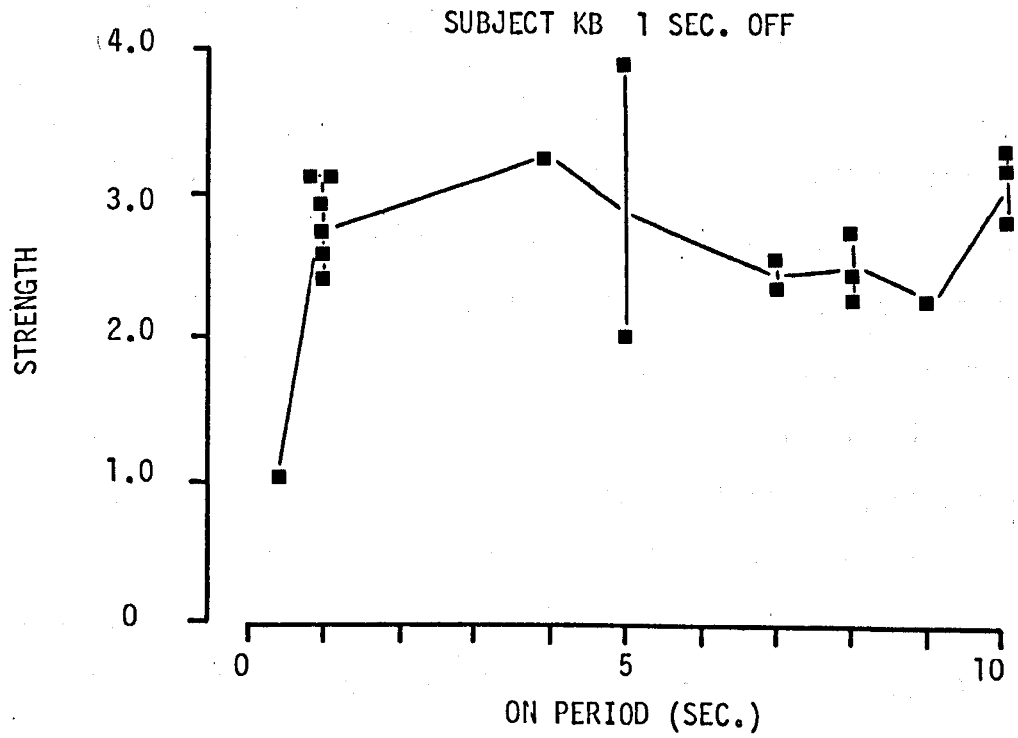
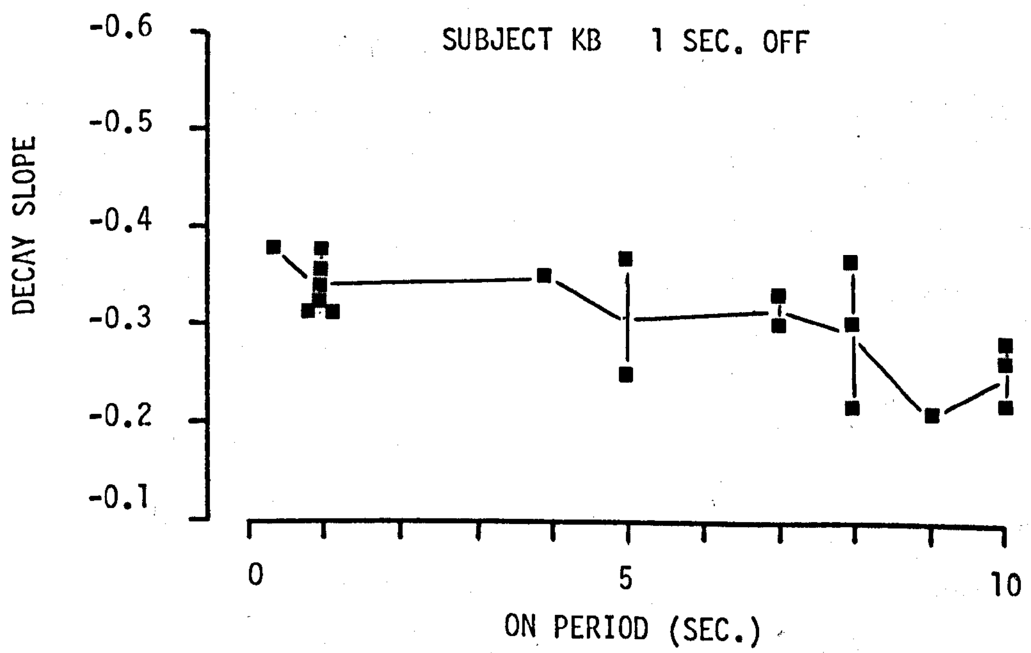

SUBJECT KB 1 SEC. OFF
STRENGTH
4.0
3.0
2.0
1.0
0
0
5
10
ON PERIOD (SEC.)

FIG. 4.8


SUBJECT KB 1 SEC. OFF
DECAY SLOPE
-0.6
-0.5
-0.4
-0.3
-0.2
-0.1
0
5
10
ON PERIOD (SEC.)

series of experiments the strength increases until the 'ON' and 'OFF' periods are equal to each other, but there is no evidence for any further systematic increase once the 'ON' becomes the longer.

(b) Decay Slope

Fig. 4.8 is the plot of decay slope against 'ON' period for this series of experiments. By contrast with the series already discussed, the decay slope values do not start off at some high level and decrease as the 'ON' period gets longer. Instead, the mean value remains fairly constant throughout the range of 'ON' periods. The level is slightly lower than for the other series at short 'ON' periods, slightly higher at intermediate 'ON' periods and about the same for the longest 'ON' period.

The graphs in Appendix G reveal that there are no results which show a marked deviation from a straight line on log-log co-ordinates, which again is in marked contrast with previously discussed results. There are none which are better fitted on linear-log co-ordinates, and these graphs are therefore not included.

4.2.4 'ON' period varied, for a constant 'OFF' period of ½ sec.

This was not originally contemplated as a series in its own right, but developed out of an emerging interest in the changes in strength and decay slope which seemed to occur as the 'OFF' was incressed from 0 to 1 sec., whatever the 'ON' period.

(a) Strength of A/E

The scatter plot showing the strength of A/E in relation to the length of the 'ON' period is shown in Fig. 4.9. The shortest 'ON' period used was ½ sec. but even with such a short duration the strength

FIG. 4.9

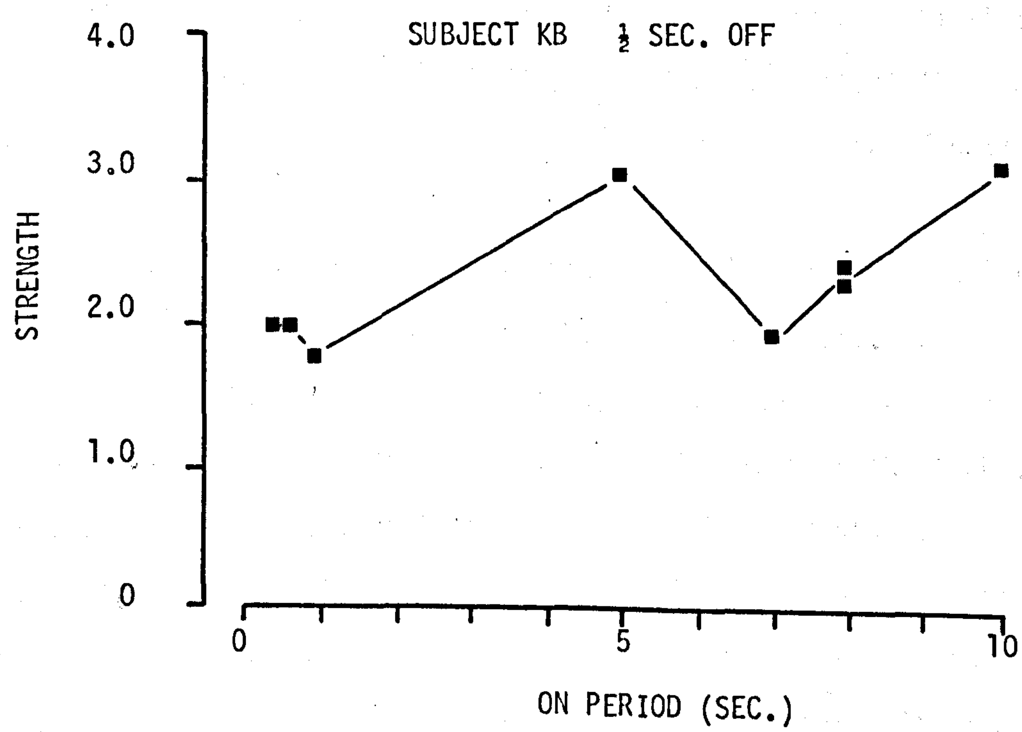
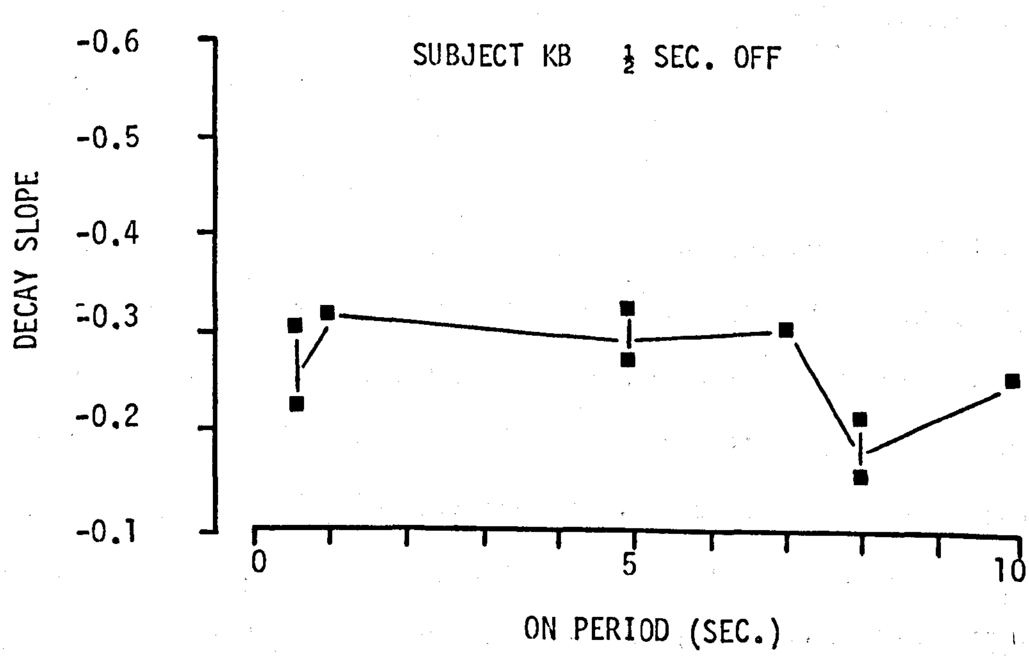


FIG. 4.10



is high. The two results are identical, and the strength at 1 sec. 'ON' is very similar. These results confirm two points already made. Firstly, the first ½ to 1 sec. of exposure has a critical influence on the initial strength. Secondly, for these short 'ON' periods, reducing the 'OFF' is associated with an increased rate of build-up of A/E strength.

For all sequences in this series the 'ON' period is equal to or greater in length than the 'OFF'. For the 1 and 5 sec. 'OFF' conditions there was no clear evidence for any systematic change in the strength once the length of the 'ON' period became longer than the 'OFF'. For this series there is very little scatter of data points, and there are some similarities with the 1 sec. 'OFF' results for the trends in the mean values. Both sets of results show higher mean values at 5 and 10 sec. 'ON' than for intermediate periods. It is difficult to account for the difference in scatter between the two series in terms of environmental conditions (e.g. repeat runs were equally scattered over a period of months, there was no real difference in the sleep patterns of the subject and runs were conducted under the same conditions and at the same time of day).

(b) Decay Slope

Fig. 4.10 shows the results for this series and is similar to that for the previous series in showing that over the middle part of the range of 'ON' periods the decay slope values are fairly constant at about -0.3. There is a distinct drop in the steepness of the decay slope at 8 sec. 'ON' in this series and 9 sec. 'ON' in the previous series. This is followed by a slight rise at 10 sec. - to -0.26 in both cases. The changes in decay slope occur at roughly similar points and are in the same direction as the observed changes in strength.

The graphs for this series (see Appendix G) show that all results are fairly well fitted by a straight line on log-log co-ordinates.

4.2.5 'ON' period varied, with no dark interstimulus interval

In principle, these experiments should provide the clearest evidence regarding the role of the 'ON' period as this is the only variable likely to affect the results (reasons have already been presented for discounting the role of the cycle duration). The whole of the adaptation duration is occupied by pattern stimulation, with no dark interval at all.

(a) Strength of A/E

The most notable feature revealed by Fig. 4.11 is the rapid rise in strength as the 'ON' period is increased from ¼ sec. to 1 sec. All three results for ¼ sec. 'ON' are quite high but clearly below the level for any of the other temporal sequences of this series. The strength builds up to a peak for 'ON' periods between ½ sec. and 1 sec. - the results for 1 sec. 'ON' are higher than those for ½ sec. 'ON', and the results for the 'ON' period of ¾ sec. overlap both. There are only slight changes associated with further increases in the length of the 'ON' period, and these may not be significant because of the amount of scatter of data points between sequences.

These results are similar to those previously discussed for this subject in showing the rapid rise in strength as the 'ON' period is increased to about 1 sec. or so. It is of interest that these changes occur when there is no change in the total duration of stimulation.

Fig. 4.11 also shows the results for a second subject (RM). There is some fluctuation in the strength for the short 'ON' periods, but it can be seen that the strength is relatively high even for ¼ sec. 'ON'

FIG. 4.11(a)

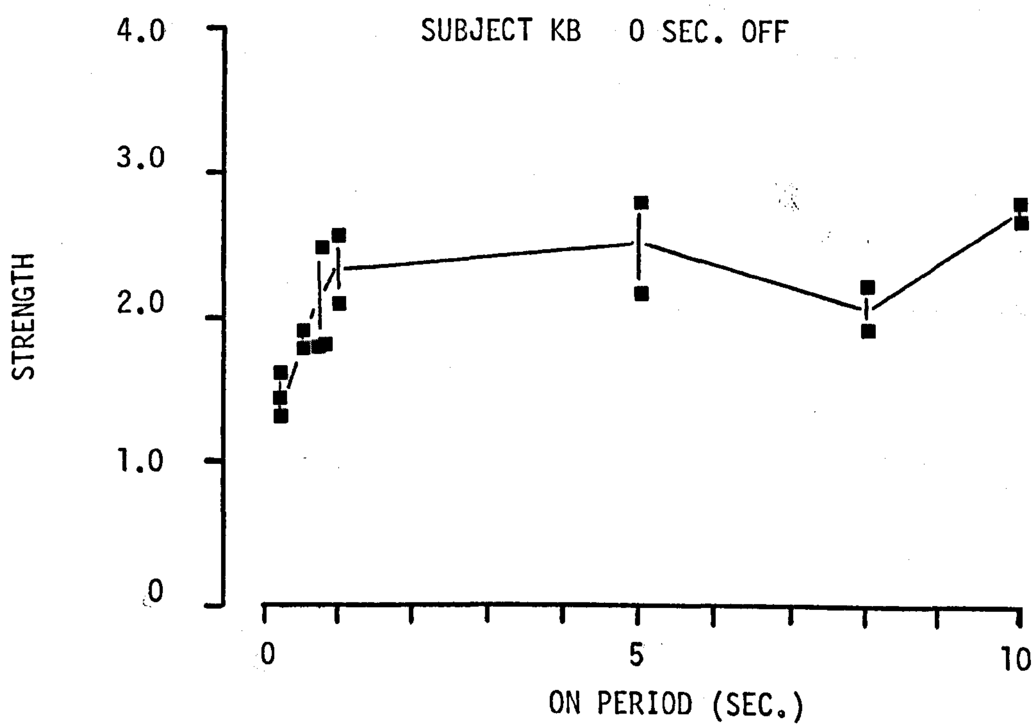
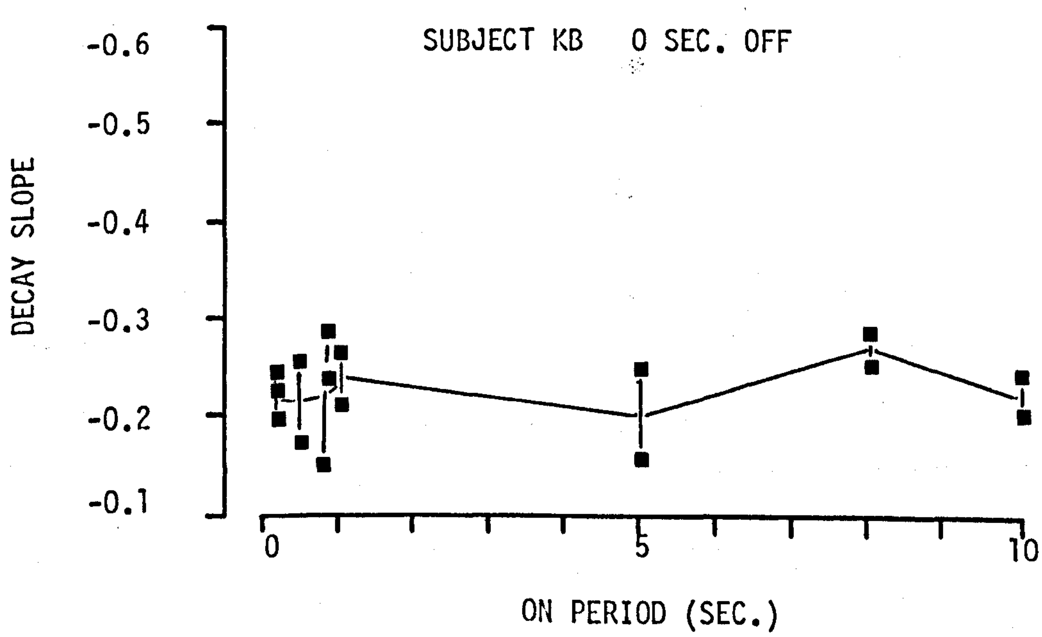
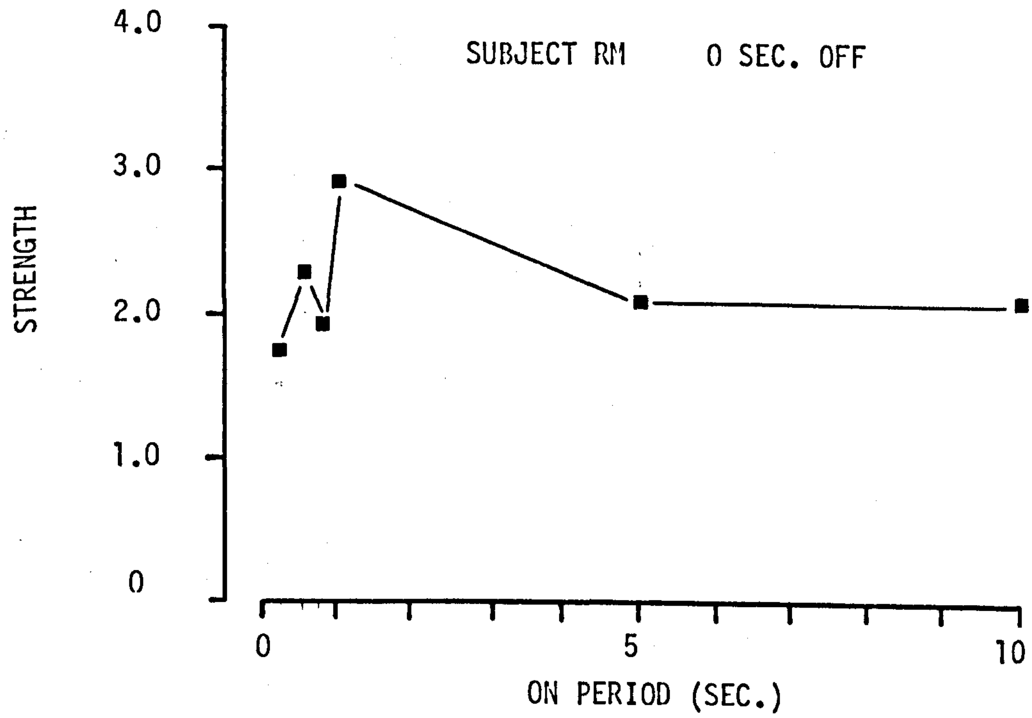


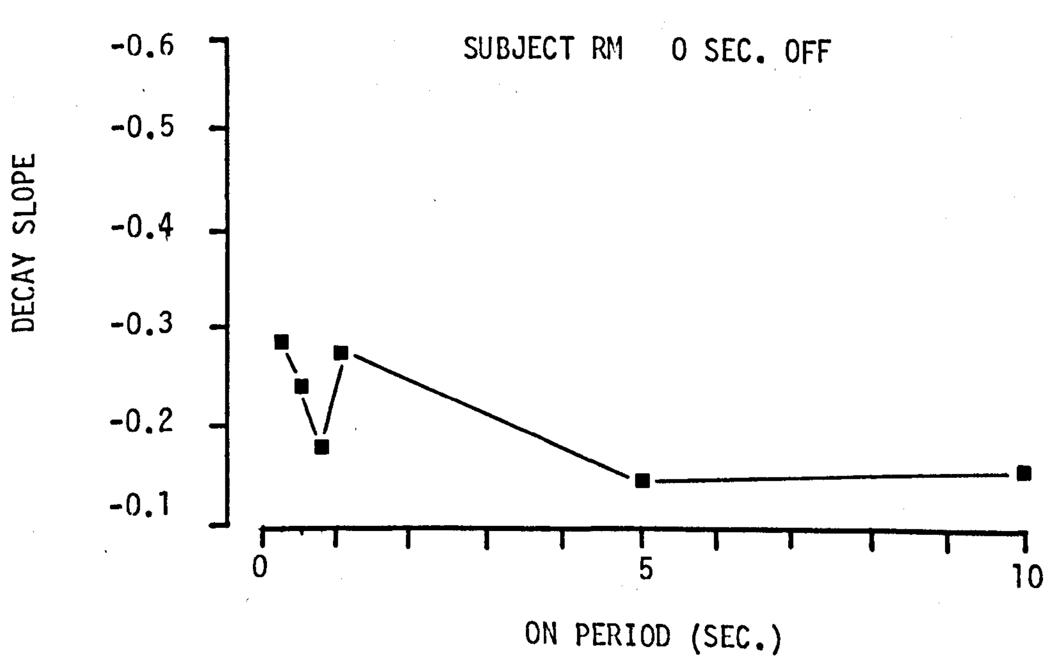
FIG. 4.12(a)



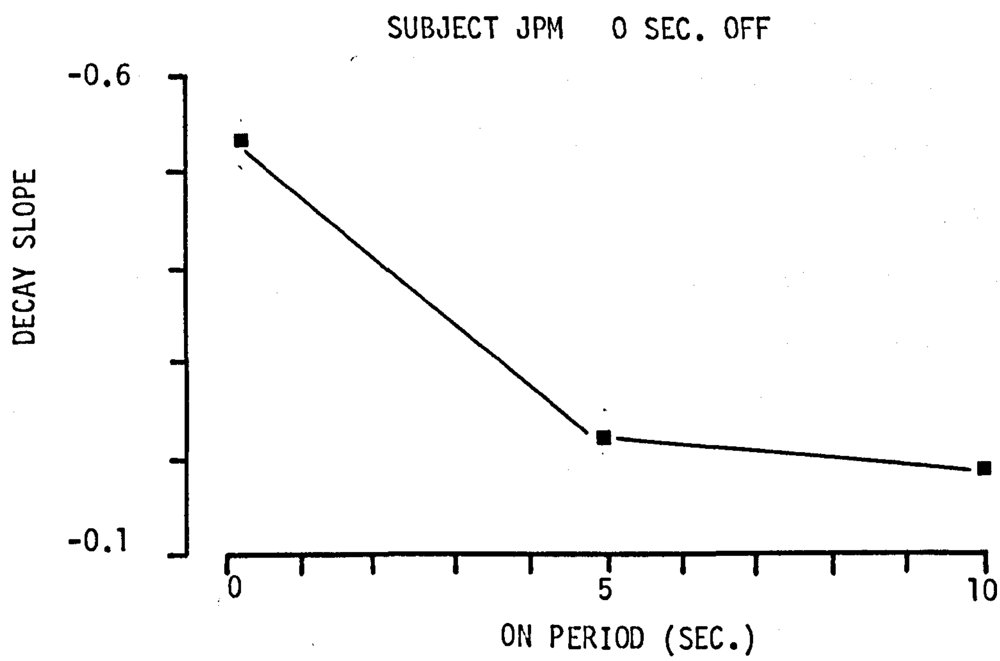
4.11(b)


SUBJECT RM 0 SEC. OFF
STRENGTH
4.0
3.0
2.0
1.0
0
0
5
10
ON PERIOD (SEC.)

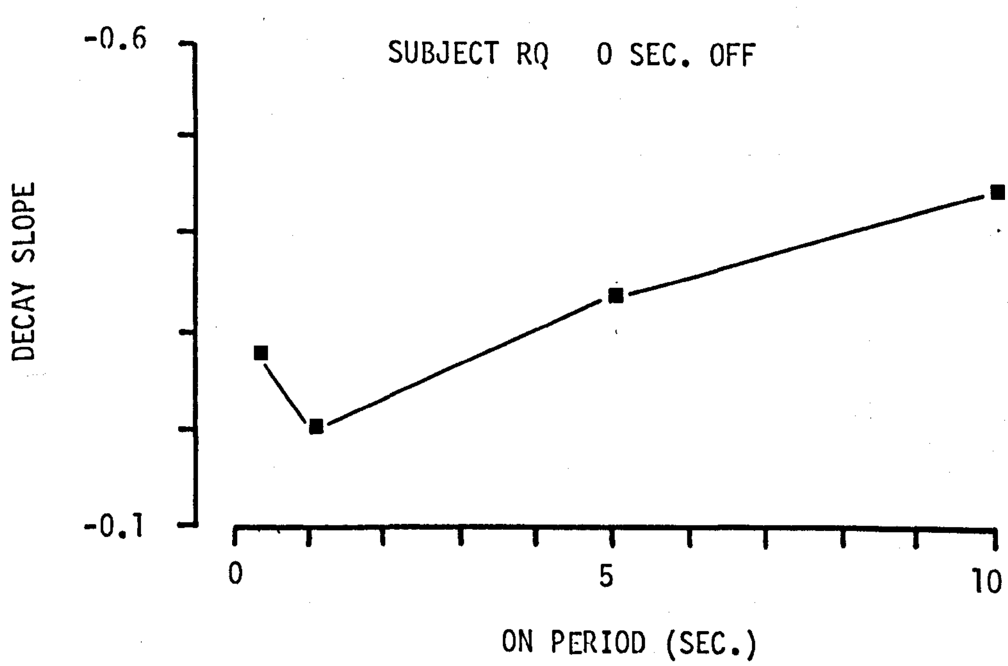
4.12(b)


SUBJECT RM 0 SEC. OFF
DECAY SLOPE
-0.6
-0.5
-0.4
-0.3
-0.2
-0.1
0
5
10
ON PERIOD (SEC.)

4.12(c)


SUBJECT JPM 0 SEC. OFF
-0.6
-0.1
DECAY SLOPE
0
5
10
ON PERIOD (SEC.)

4.12(d)


SUBJECT RQ 0 SEC. OFF
-0.6
-0.1
DECAY SLOPE
0
5
10
ON PERIOD (SEC.)

periods and rises rapidly, peaking for 'ON' periods of 1 sec. In comparison with subject K.B., there is then a slight fall in the strength at 5 sec. 'ON' after which there is no further change. Table 4.4 shows the strengths over a restricted number of experiments for two further subjects. Subject R.Q. shows the expected build up to 1 sec. 'ON' but, unlike the other two subjects discussed, his A/E rises rapidly again at 5 sec. 'ON' and 10 sec. 'ON' to a strength which is outside the range of the measuring apparatus. For subject J.P.M. the strength is beyond the measurable range for 'ON' periods of ¼ sec. and 10 sec. but is at a lower level for the 5 sec. 'ON' sequences. This may indicate random fluctuation or that this subject shows a more rapid build-up to the maximum strength.

TABLE 4.4

ON (sec.)	R.Q.	J.P.M.
¼	1.4	?
1	1.7	-
5	?	2.0
10	?	?

(b) Decay Slope

Fig. 4.12 shows that for this series of experiments there is no systematic variation in the decay slope correlated with changes in the 'ON', for subject K.B. The line connecting the mean values remains fairly flat with an average value of -0.23. The average level of the line is therefore lower than that for the sequences with ½ and 1 sec. 'OFF' periods.

The results for the other subjects are not in full agreement. For R.M. there is some variability for 'ON' periods of 1 sec. or less but the graph levels-off at 5 and 10 sec. 'ON'. It is difficult to comment too much on the results for J.P.M. and R.Q. because the regression values for four of the sequences are derived from experiments in which the initial strength was not measurable, and the statistical analysis indicated that calculating the decay slope when the first point is later than that at 1 min. would be likely to yield steeper slopes. Inspection of the graphs in Appendix G will show that there are no obvious deviations from a reasonable fit to a straight line on log-log plot. This is an obvious difference from the results for the 10 sec. 'OFF' period.

4.2.6 <u>Summary of results from experiments in which the 'ON' period is the independent variable</u>

(a) Strength of A/E

(i) Systematic changes in the strength of the A/E correlate with changes in the length of the 'ON' period. 'ON' periods of length up to about 1 sec. or so exert the most critical influence, whatever the 'OFF' period.

(ii) The rate of increase in strength over this range of critical 'ON' periods varies from one series to the next. Shorter 'OFF' periods are in the main associated with a more rapid rise in strength.

(iii) The point at which the strength levels off varies from one series to the next. The ON:OFF ratio may be a critical parameter.

(b) Decay Slope

(i) There are no factors which are common to all the series - that is, changes in the 'ON' do not have the same effect on the decay slope at all 'OFF' values.

(ii) The two sequences with relatively long 'OFF' periods show a clear decrease in the level of the decay slope as the 'ON' increases, the critical period of transition being somewhere in the range of 'ON' periods between 2 and 5 sec. These changes in decay slope correspond to a period of transition from non-linear to linear decay when the data are plotted on log-log co-ordinates.

(iii) The results for certain of these sequences may be better fitted by a straight line on a plot with linear-log co-ordinates.

(iv) There are differences in overall level for the decay slope for different series: the lowest is with 0 sec. interstimulus delay, and the highest when there is a ½ or 1 sec. dark interval.

(c) Strength and Decay Slope

(i) There are a number of occasions when initial strength varies while the slope remains stable. For example, strength varies with no change in slope for the series with a 0 sec. 'OFF' period; and increase in strength continues when there are no further changes in decay slope for the 10 sec. OFF series.

(ii) The implication would seem to be that the factors underlying changes in strength are separate from and have a different time course to those related to the rate of decay.

(iii) Although there are some common features between the different series which correlate with changes in the length of the 'ON' period, the fact that there are differences must imply that the 'ON' period is not the only factor underlying the observed changes - the length of the 'OFF' must also exert an influence.

4.3. Experiments in which the 'OFF' period is the independent variable for a number of constant 'ON' periods

The experiments reported in this section fall into two groups. Firstly, those in which interest was in possible changes over a range of 'OFF' periods from 0 to 10 sec. (series with 'ON' periods of 10; 5, 1 and ½ sec.) and, secondly, those in which interest was centred on the restricted part of the range between 0 and 1 sec. 'OFF' (series with 8 and 7 sec. 'ON' periods). Obviously, the first group overlap the second to some extent, but it will be convenient to consider the experiments under these two groupings.

4.3.1 'OFF' period varied, for a constant 'ON' period of 10 sec.

(a) Strength of A/E

Fig. 4.13 is the scatter plot for this series for subject K.B. It can be seen that there are clear changes in the strength associated with increase in the length of the 'OFF' period from 0 to 10 sec. Although there is slight overlap of the data points, there is fairly strong evidence for a rise in the strength with increase in the 'OFF' up to 1 sec. There is then a sharp drop when the 'OFF' is further increased to 2 sec. to a level well below that for the sequences with shorter 'OFF' periods. This is followed by a steady rise in the strength as the 'OFF' period is increased to 5 and 10 sec.

Table 4.5 shows the results for three other subjects over a restricted number of experiments. The results for subject M.Y. are similar to K.B.'s in showing higher values at 1 and 10 sec. 'OFF' than at

TABLE 4.5. Strength of A/E for three sequences of stimulation

Sequence			Subjects		
ON (sec.)	OFF (sec.)		M.Y.	D.B.	C.M.J.
10	1		?	?	2.1
10	5		3.5	2.9	1.9
10	10		?	2.1	1.7

5 sec. 'OFF', the strength of the A/E in the former case going outside the range of the measuring apparatus. The results for the other two subjects are in agreement in showing a high strength at 1 sec. 'OFF' with a decrease in strength when the 'OFF' is increased to 5 sec. However, they differ in showing a further decrease when the 'OFF' is extended to 10 sec. In short, there is agreement among the subjects' results for two of the conditions, but variation in the trend between 5 and 10 sec. 'OFF'.

(b) Decay Slope

Fig. 4.14 shows the scatter of decay slopes for subject K.B. It

FIG. 4.13

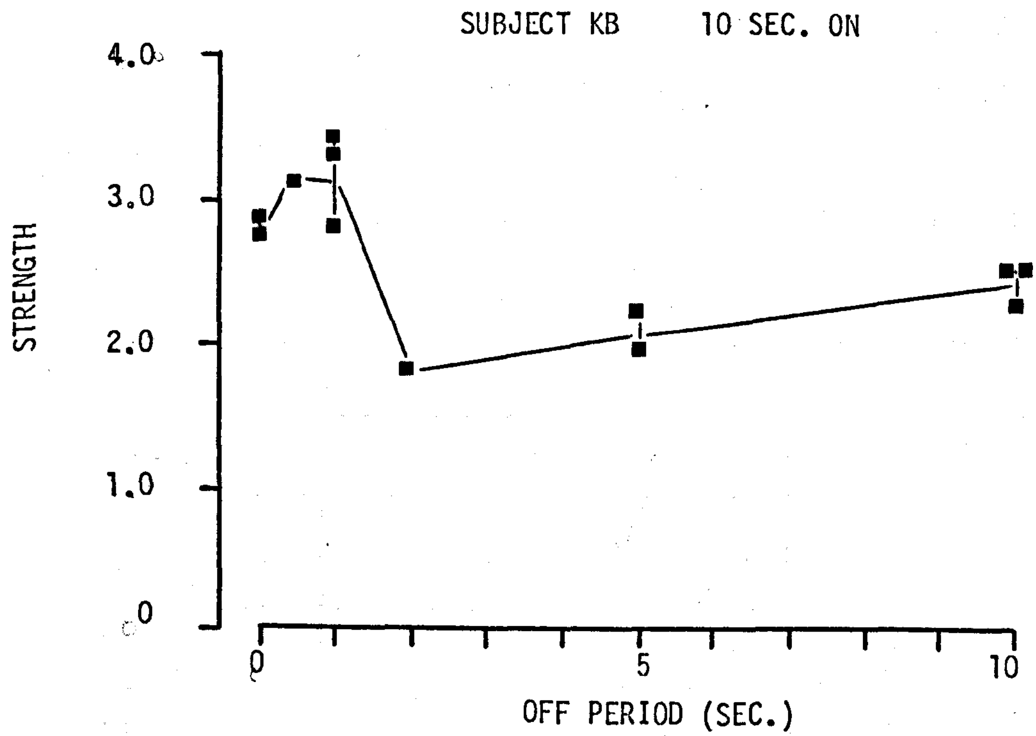
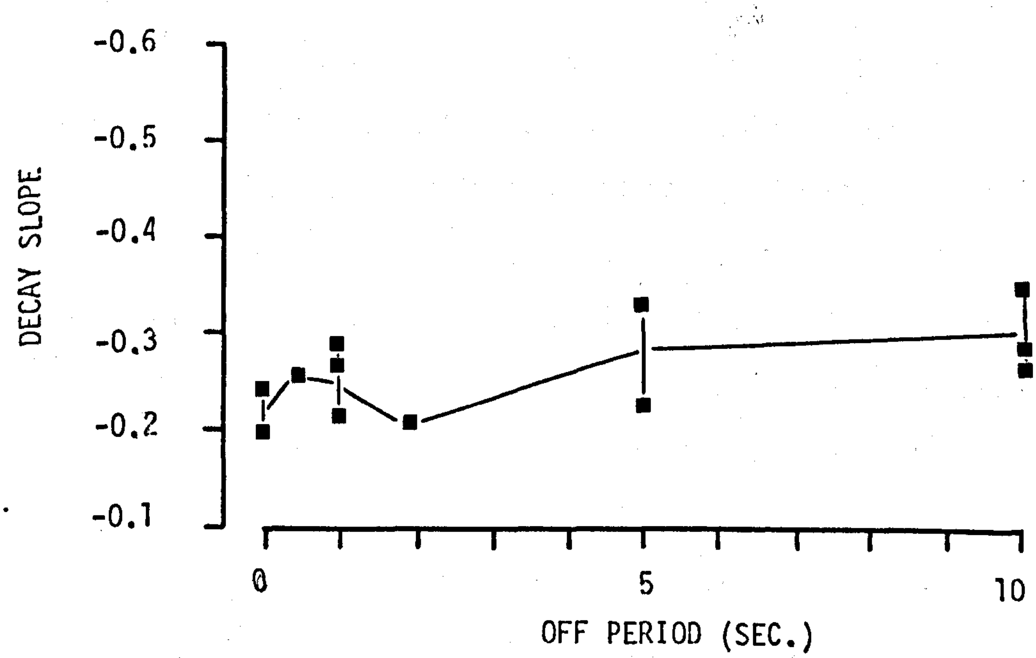


FIG. 4.14



can be seen that there are similar trends in the changes in the decay slope to those observed with respect to changes in the initial strength. However, the mean differences between sequences are small and there is sufficient scatter of data points to make one uncertain as to the significance of these changes.

Table 4.6 shows the results for the other subjects, and these confirm

TABLE 4.6. Decay Slope for three sequences of stimulation

Sequence			Subjects		
ON (sec.)	OFF (sec.)		M.Y.	D.B.	C.M.J.
10	1		(0.34)	0.26	0.15
10	5		0.26	0.14	0.20
10	10		(0.32)	0.14	0.20

( ) Indicates that the regression value is derived from statistics with the first point at some value greater than 1 min.

the difficulty of deducing any clear trends. The results for M.Y. for two of the sequences are estimated values from analysis which has the first reading later than 1 min. after the end of exposure. These two results are therefore likely to be biased on the high side relative to the results in which a reading could be obtained at 1 min. The results for subject D.B. and C.M.J. are similar at 5 and 10 sec. 'OFF', but both differ from the 1 sec. 'OFF' sequence. However, in one case there is a reduction and in the other an increase so the changes are not likely to be significant. The graphs for all subjects for each sequence are shown in Appendix G, and it can be seen that there are no systematic deviations from linearity on log-log co-ordinates.

4.3.2 'OFF' period varied, for a constant 'ON' period of 5 sec.

Fig. 4.15 shows the strength correlated with the length of the 'OFF' period. The results for subject K.B. show a clear rise in strength as the 'OFF' period is lengthened from 0 to ½ sec. There is no change in the mean value at 1 sec. 'OFF' but there is a considerable difference in strength between the two experiments with this sequence. There is then a sharp decline in strength at 2 sec. 'OFF', to a level clearly below that for the 0 or ½ sec. 'OFF' sequences but overlapping the results for the 1 sec. 'OFF' sequence. There is no change as the 'OFF' is increased to 5 sec., but when the 'OFF' becomes longer than the 'ON' - at 10 sec. - there is a decrease in strength.

The results for the other two subjects, also shown in Fig. 4.14, illustrate features which are in some ways similar to those for subject K.B., but which in other significant ways are dissimilar. Both show a build-up as the 'OFF' period is lengthened beyond 1 sec., peak strength occurring when the 'OFF' period is 2 sec. followed by a sharp decrease as the 'OFF' period is further increased to 3 sec. Subject K.B. shows the peak at ½ or 1 sec. 'OFF' and the decrease at 2 sec. This could be an inter-subject difference of some considerable interest. Further increases in the 'OFF' period beyond 3 sec. are associated with changes that are not in full agreement with each other. For subject C.M.J. the strength is the same at 5 and 10 sec. 'OFF', but D.G. shows a decrease at 5 sec. followed by a further decrease at 10 sec. 'OFF'.

(b) Decay Slope

Fig. 4.16 shows the derived values for the decay slope for this series for subject K.B. It can be seen that there is a clear increase

FIG. 4.15(a)

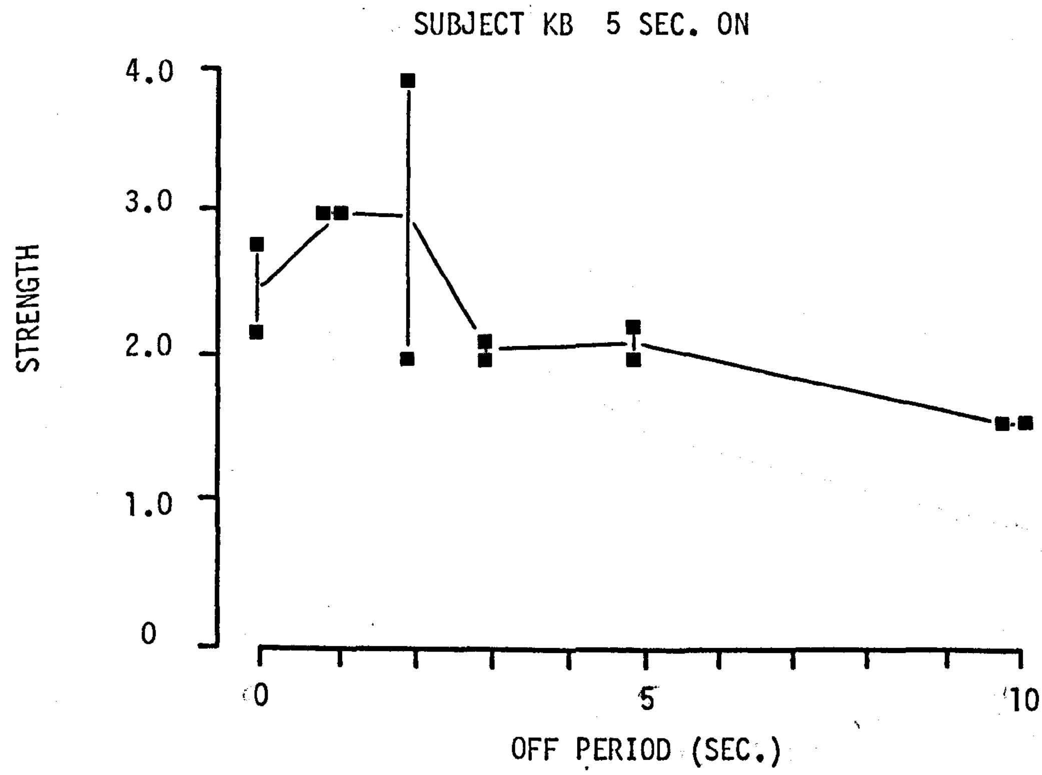
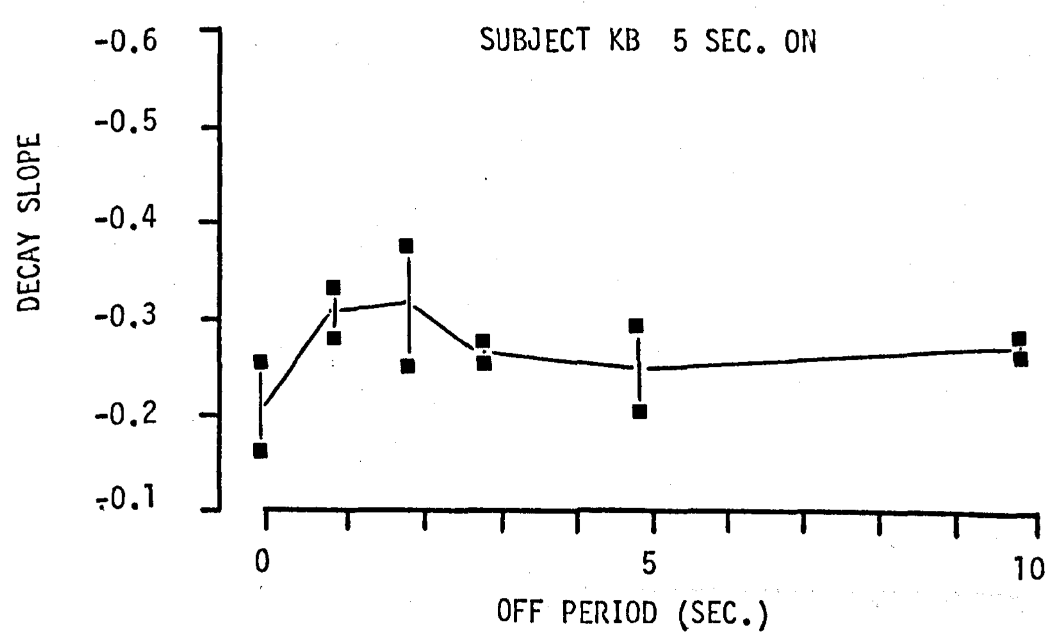
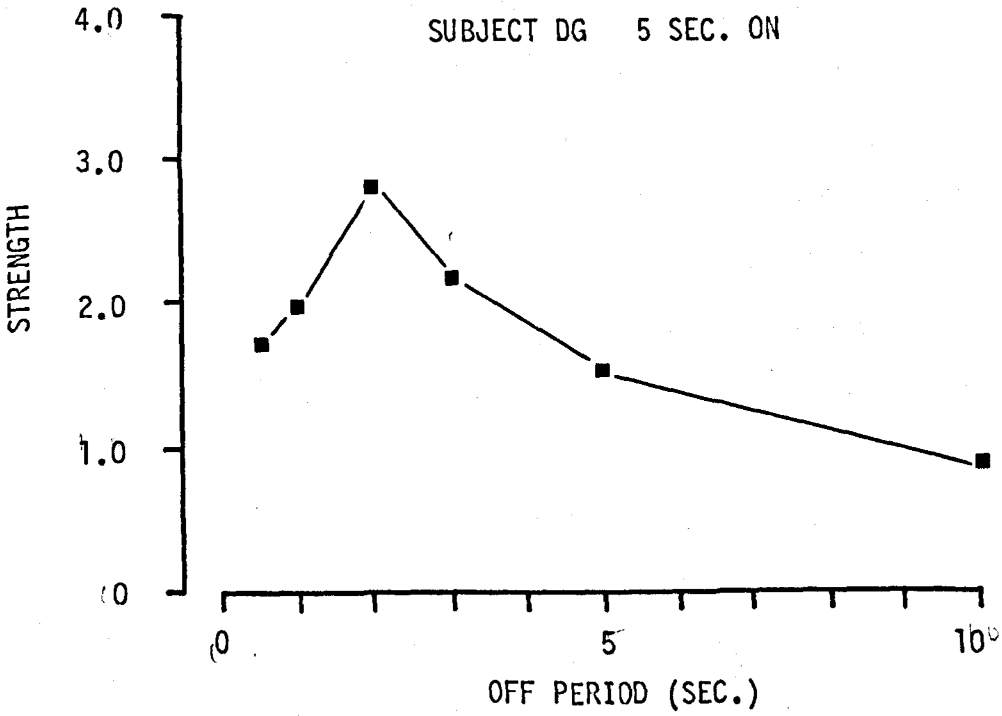


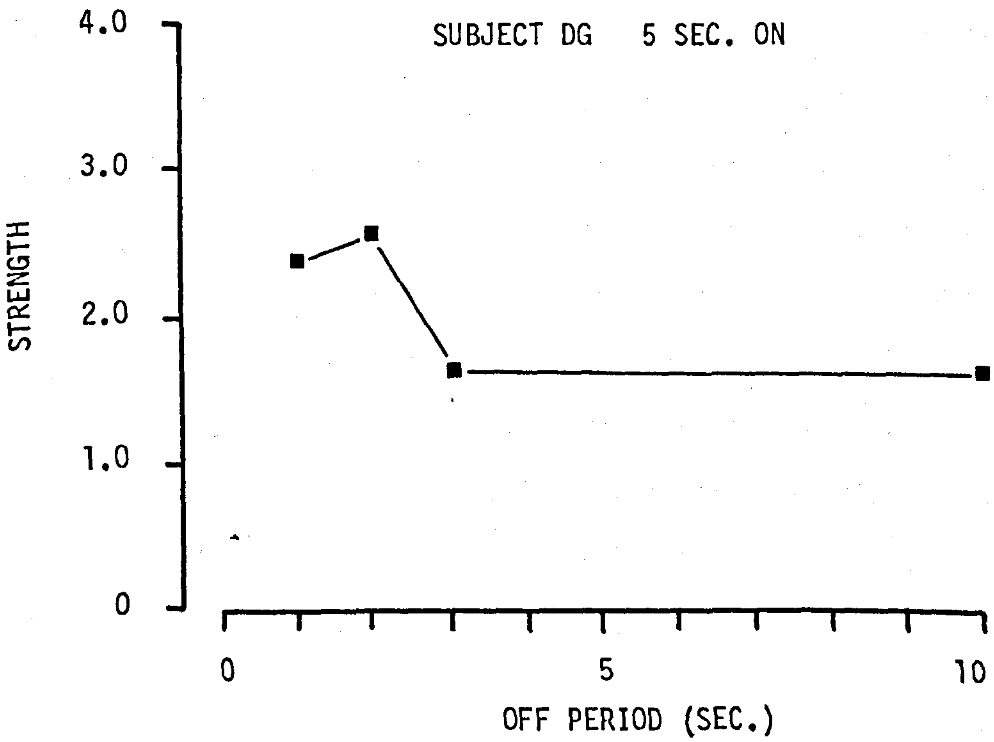
FIG. 4.16



4.15(b)


SUBJECT DG 5 SEC. ON
STRENGTH
4.0
3.0
2.0
1.0
0
0
5
10
OFF PERIOD (SEC.)

4.15(c)


SUBJECT DG 5 SEC. ON
STRENGTH
4.0
3.0
2.0
1.0
0
0
5
10
OFF PERIOD (SEC.)

in the decay slope as the 'OFF' period is lengthened from 0 sec. to ½ sec. with no overlap of the data points. There is virtually no change as the 'OFF' is increased again to 1 sec. There is then a drop in the mean level at 2 sec. 'OFF', the results for the two experiments being very similar. The level is clearly below that for the ½ sec 'OFF' sequence. The sequence of changes of the decay slope mimic those observed for the strength of the A/E. It is also of interest that the sequence of changes in the decay slope is identical with that for the previous series of experiments. Similarly, in this case there is no significant change when the 'OFF' is increased to 5 and to 10 sec.

Most of these experiments were conducted on a brief return visit to Keele when the time of the experimenter and the volunteer subjects was limited, and it was unfortunately not possible to follow the decay for subject D.G., nor for one of the four sequences for C.M.J. The results for C.M.J. show a slight decrease in the decay slope as the 'OFF' is increased from 1 to 2 sec. followed by a slight rise again with further increase of the 'OFF' to 10 sec. The trends are the same as for K.B., but the differences between sequences are only slight. Table 4.7 shows these results, together with comparable results for subject K.B. It would be extremely interesting to confirm whether other subjects would show similar changes in the decay slope. The results for C.M.J. raise the possibility that the trends would be observed and that the points of change are identical with those for K.B. It should be remembered that the peak in strength for this subject occurred at a different point to that for K.B. (i.e. the peak strength occurred with a 2 sec. 'OFF' period and dropped sharply with further increase to 3 sec. 'OFF'). In other words, one would like to know whether the point

TABLE 4.7. Decay Slopes for three temporal sequences

Sequence			Subjects	
ON (sec.)	OFF (sec.)		K.B.	C.M.J.
5	1		-0.31	-0.25
5	2		-0.26	-0.22
5	10		-0.27	-0.24

of change in strength is always the same as that for change of decay slope, or whether the points of transition may differ. The graphs of results in Appendix G show that the data for two of the sequences show a very good fit to a straight line on log-log plot and that for the series as a whole there are no obvious variations to suggest that any of the results would be fitted better on other co-ordinates.

4.3.3 'OFF' period varied, for a constant 'ON' period of 4 sec.

Only three experiments are included in this series. The main questions in mind were: (i) how do strength and decay slope change (if at all) when the 'OFF' is increased from 1 sec to 2 sec and (ii) when the 'OFF' is 1 sec., how does strength vary as the 'ON' period is increased - is there a 'peak' at about 4 or 5 sec.? This second point was discussed earlier, and we will be concerned here only with the former.

The results are summarised in Table 4.8. The two sequences just discussed (i.e. 10 sec. 'ON' and 5 sec. 'ON') showed a drop in strength when the 'OFF' was increased from 1 to 2 sec., and this phenomenon is

TABLE 4.8. Subject K.B.

OFF (sec.)	Strength	Decay Slope
1	3.3	-0.35
2	2.7	-0.29
10	1.5 1.3	-0.34 -0.23

clearly confirmed here. The impression is that overall there is a steady decline in strength to 10 sec. 'OFF', but one cannot be sure - there may, for example, be a plateau up to 4 sec.'OFF', followed by a steady decline. Equally, the other two series show a decrease in the decay slope, which is also evident in this case. There is no change in the mean value with increase to 10 sec.'OFF' (-0.29 in both cases), but the difference between the two results makes it difficult to draw firm conclusions about the real significance of these changes for the series as a whole.

4.3.4 'OFF' period varied, for a constant 'ON' period of 1 sec.

Fig. 4.17 suggests that there may be similar changes in the strength for a 1 sec.'ON' period when the 'OFF' period is varied from 0 to 1 sec. In this case the changes are not identical with those already discussed, in that the strength correlated with the ½ sec.'OFF' sequence is lower than that with no interstimulus delay. However, the strength again reaches a peak when the 'OFF' is 1 sec. and there is very little overlap of the data points with those for the sequence with no interstimulus delay. It is of interest that this increase occurs in this series of

FIG. 4.17

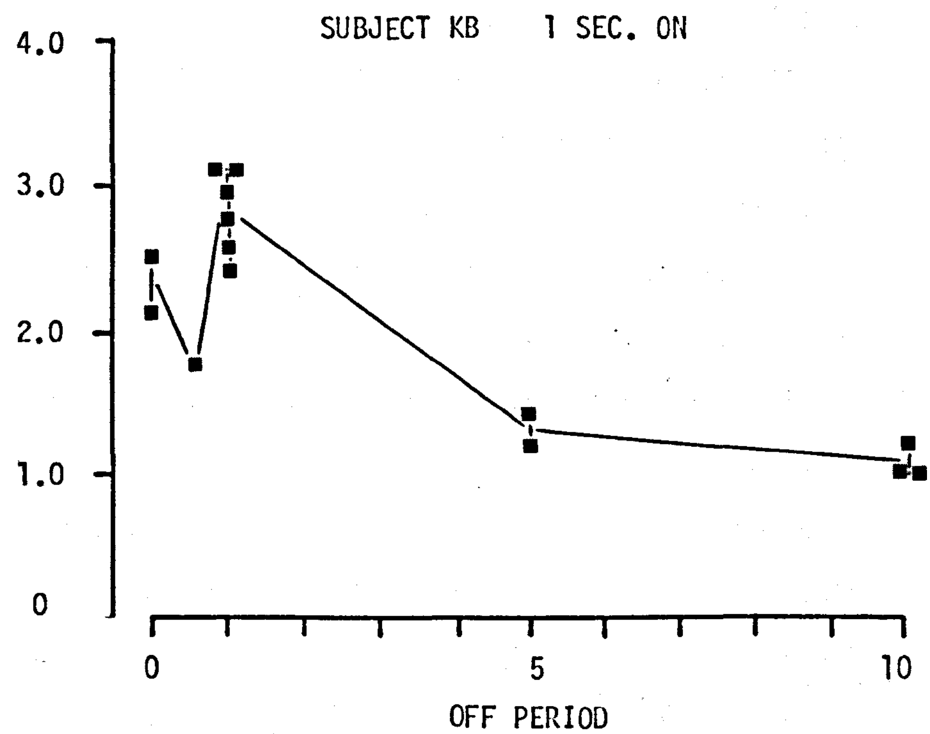
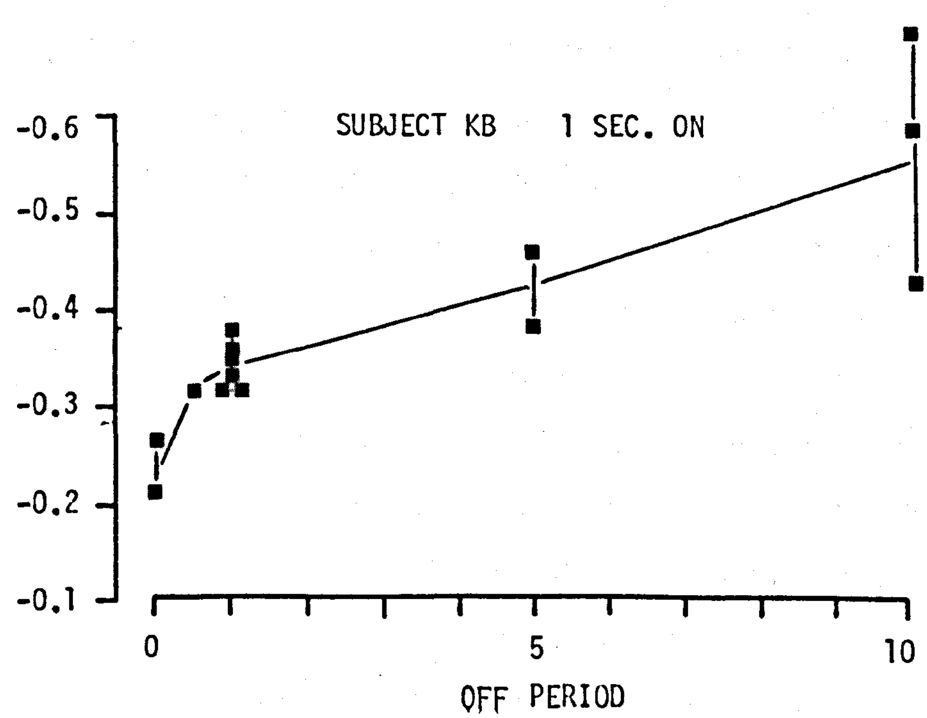


FIG. 4.18

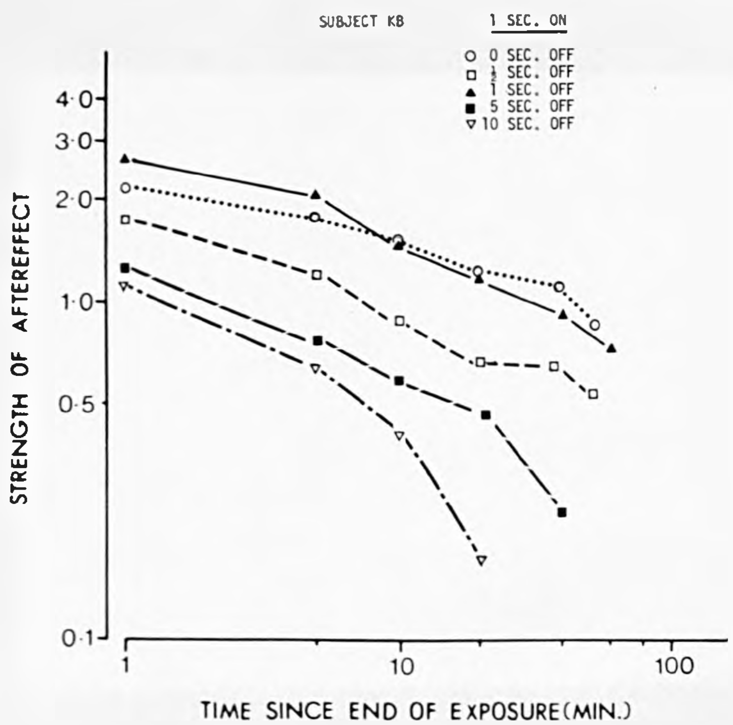


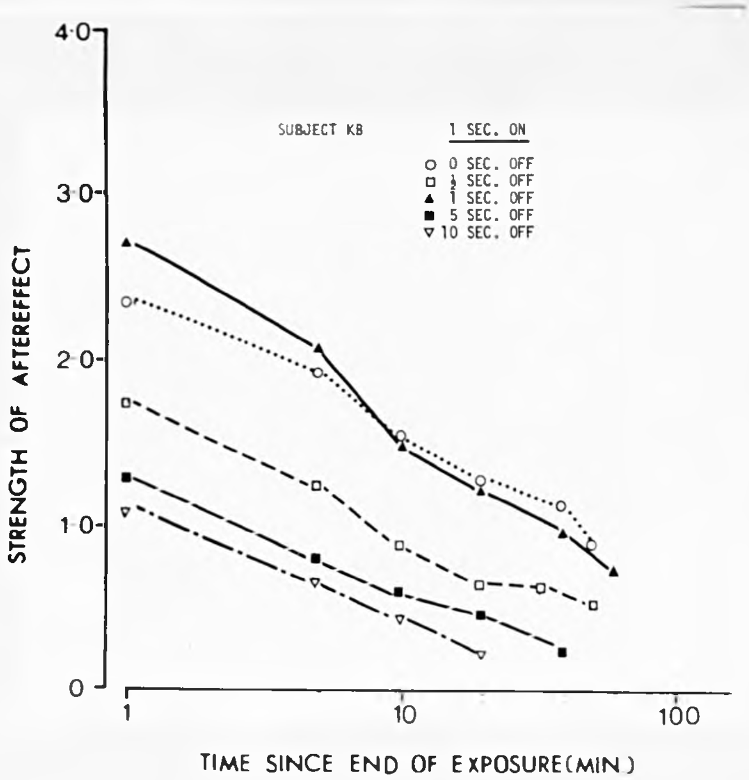
experiments even though there is a considerable reduction in the total exposure time - with 0 sec. 'OFF' the whole of the 15 min. is occupied by pattern stimulation, but when the 'OFF' period is 1 sec. this time has been cut by 50%. At this point the 'ON' and the 'OFF' are equal. As one would expect on the basis of the results already discussed, further increase in the length of the 'OFF' period is associated with a reduction in strength. It can be seen that the strength is quite substantially reduced when the 'OFF' period is 5 sec., to less than half that at 1 sec. 'OFF'. The results for the series already described would imply that the largest drop in strength would occur when the 'OFF' is increased from 1 sec. to 2 sec. This drop ought to be independent of the change in the ratio of 'ON' to 'OFF' periods. It would be of interest to confirm this point. Finally, increase in the length of the 'OFF' period to 10 sec. is associated with a further slight decrease in strength.

(b) Decay Slope

Fig. 4.18 shows the changes in the decay slope associated with increase in the length of the 'OFF' period. There is a clear, substantial rise in the calculated slope of the decay line for only a short increase in the 'OFF' from 0 to ½ sec., followed by a smaller increase in the mean level when the 'OFF' is 1 sec. Thereafter, there is a steady rise in the mean level, with some overlap of the individual data points, as the 'OFF' is further increased to 5 and then to 10 sec. It would be of considerable interest to know if there is any change in the decay slope when the 'OFF' is increased from 1 to 2 sec. in view of the results already discussed. It would also be of interest to determine the strength at these timing values, in relation to the question of the similarity in the trends of

FIG. 4.19


SUBJECT KB
1 SEC. ON
0 SEC. OFF
½ SEC. OFF
1 SEC. OFF
5 SEC. OFF
10 SEC. OFF
STRENGTH OF AFTEREFFECT
4·0
3·0
2·0
1·0
0·5
0·1
1
10
100
TIME SINCE END OF EXPOSURE(MIN.)


SUBJECT KB
1 SEC. ON
0 SEC. OFF
½ SEC. OFF
1 SEC. OFF
5 SEC. OFF
10 SEC. OFF
STRENGTH OF AFTEREFFECT
4·0
3·0
2·0
1·0
0
1
10
100
TIME SINCE END OF EXPOSURE(MIN.)

changes in strength and decay slope.

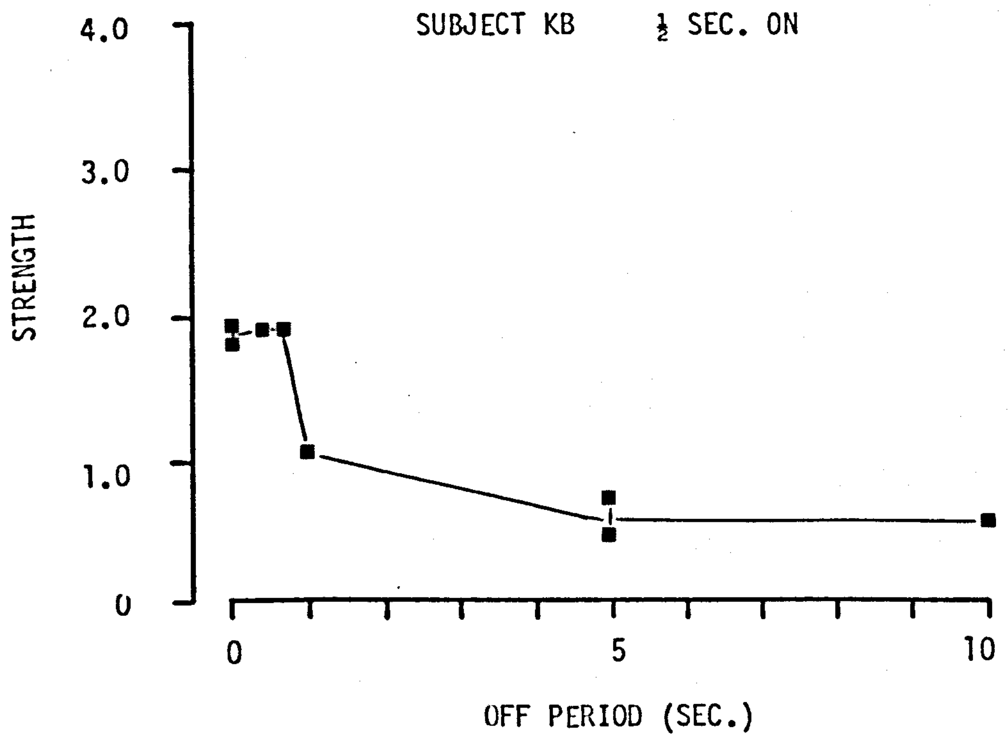
The graphs in Appendix G show interesting changes in the shape of the plots on log-log co-ordinates. The results for the whole series are reproduced in Fig. 4.19, the scatter bars being omitted for clarity. The same results are also shown on linear-log plot. The three results with the shorter 'OFF' periods (0, ½ and 1 sec.) are perhaps slightly better fitted on log-log, certainly over the range 5 to 60 min. However, for 'OFF' periods of 5 and 10 sec. it can be seen that there is a clear curve to the plot on log-log co-ordinates, but that a good fit to a straight line is obtained on the linear-log plot. The change in shape must therefore begin at some point when the 'OFF' is longer than 1 sec. The process of change would seem to be progressive as the 'OFF' period is increased in length, though the data are rather limited on this point.

4.3.5 'OFF' period varied for a constant 'ON' period of ½ sec.

(a) Strength of A/E

The plot of the strength related to the length of the 'OFF' period is shown in Fig. 4.20. The strength of the A/E is fairly stable for 0 and ½ sec. 'OFF', the overall level being on the low side compared with others in this group, which may be related to the short 'ON' period. When the length of the 'OFF' is increased to 1 sec. the strength is much lower, the decrease being about one half for this further lengthening of the 'OFF' by ½ sec. It is of interest that this sharp drop should occur at the point at which the 'OFF' period becomes longer than the 'ON'. This same phenomenon has been mentioned in relation to the series with 4, 5 and 10 sec. 'ON' periods, and for this subject occurred when the 'OFF' period was increased from 1 to 2 sec. Again, it would be of interest to

FIG. 4.20



determine the strength for a 2 sec. 'OFF' period. In this case, further lengthening of the 'OFF' is associated with only a slight reduction in strength. The decrease is less for longer 'OFF' periods. No other subjects took part in this series.

(b) Decay Slope

The graphs in Appendix G show that when the 'OFF' period is 5 sec. the strength of the A/E has decayed to less than 0.1 after 5 minutes, which makes it impossible to calculate a meaningful decay slope for this sequence. For the sequence with a 10 sec.'OFF' period, no readings were made beyond that at the 1 min. point. The results for the other three sequences of this series are summarised in Table 4.9. There is a slight

TABLE 4.9. Subject K.B. Series with ½ sec.'ON' period

'OFF'	Decay Slope
0	-0.17 -0.26
½	-0.30 -0.22
1	-0.37

increase in the mean value as the 'OFF' is lengthened from 0 sec. to ½ sec. and then a much sharper increase at 1 sec. 'OFF'. Obviously, the decay is even more rapid when the 'OFF' period is 5 sec. The graphs show that there is a progressive change in the shape of the plot, decay becoming non-linear on log-log plot when the 'OFF' period is 1 sec.

4.3.6 'OFF' period varied between 0 and 1 sec. for 'ON' periods of 7 and 8 sec.

The purpose of this group of experiments was to provide additional evidence regarding the process of change as the 'OFF' is increased up to 1 sec., and also related to the changes for the series of experiments in which the 'OFF' period is 1 sec. and the 'ON' period the variable. It is only the former with which we are now concerned, the latter point having been discussed earlier in this Chapter. The results are summarised in Table 4.10. For the 7 sec.'ON' series there is a clear

TABLE 4.10. Subject K.B.

OFF	7 sec.'ON'		8 sec.'ON'	
(sec.)	Strength	Decay Slope	Strength	Decay Slope
0			2.2 1.9	-0.29 -0.26
½	1.9	-0.30	2.4 2.3	-0.21 -0.16
1	2.6 2.4	-0.34 -0.30	2.3 2.5 2.8	-0.37 -0.22 -0.30

increase in the strength but virtually no change in the decay slope. For the 8 sec.'ON' series there is a very slight increase in the mean strength, but an unexpected change in the decay slope. The results for the 0 and 1 sec.'OFF' sequences are very similar, but both results for the ½ sec.'OFF' sequence are less than those for the others. This result is 'anomalous' since the changes occurring for other similar series tend to show an increase, or no change. It is therefore difficult to be certain as to the significance of these changes.

4.3.7 Summary of results from experiments in which the 'OFF' period is the independent variable

(a) Strength of A/E

(i) Most series show a build up in strength as the 'OFF' period is increased from 0 to 1 sec. though there are exceptions - chiefly for the series with the two shorter 'ON' periods.

(ii) There is evidence for a sharp drop in the strength associated with lengthening the 'OFF' period from 1 to 2 sec. (one subject) or from 2 to 3 sec. (two subjects). Again there are exceptions, for the ½ sec.'ON' series a sharp drop occurring when the 'OFF' is increased from ½ to 1 sec.

(iii) The changes in strength associated with increase in the 'OFF' beyond 1 sec. are not consistent for different series. The 10 sec.'ON' series shows a slight increase as the 'OFF' is increased from 2 to 10 sec. The 5 sec.'ON' series shows a 'plateau' as the 'OFF' is increased from 2-5 sec. followed by a decrease. The ½ and 1 sec. series show a progressive decrease, though in the former case the decrease occurs beyond ½ sec.'OFF'.

(iv) A 1 sec.'OFF' period (or 2 sec. for some subjects) appears to be a critical interstimulus period affecting strength. Beyond this, the strength seems to be affected by changes in the length of the 'OFF' relative to the 'ON' period, decrease occurring only when the 'OFF' is longer than the 'ON'.

(b) Decay Slope

(i) The changes in the strength associated with variation in the 'OFF' period from 0 to 2 sec. or so, are mimicked by the changes in the decay slope. Generally, there is a build up as the 'OFF' is increased to ½ or 1 sec. which is followed by a decrease when the 'OFF' is 2 sec.

(ii) The changes related to variation in the 'OFF' between 2 and 10 sec. are not consistent from one series to the next, and do not always change in the same way as the strength. For the 10 sec. 'ON' period, there is a slight increase in the decay slope, but for the 5 sec. 'ON' series there is no change. The 1 sec. and ½ sec. 'ON' series are associated with increase in the decay slope as the 'OFF' is increased, and these correlate with a change in the shape of the plot. The results for certain sequences are better fitted on linear-log plot.

(c) Strength and Decay

(i) In some situations the changes in strength mimic those of the changes in the 'OFF'; in other cases they both change but in opposite directions; finally, there are occasions in which only one varies.

(ii) The fact that the changes are not consistent from one series to the next must indicate that the 'OFF' is not the only variable affecting the results. In association with the previous results, it appears that both parameters have an influence.

4.4. The role of the 'ON' to 'OFF' ratio

The experiments reported in this section fall into two groups. In the first series the ON/OFF ratio is constant but the 'ON'

FIG. 4.21(a)

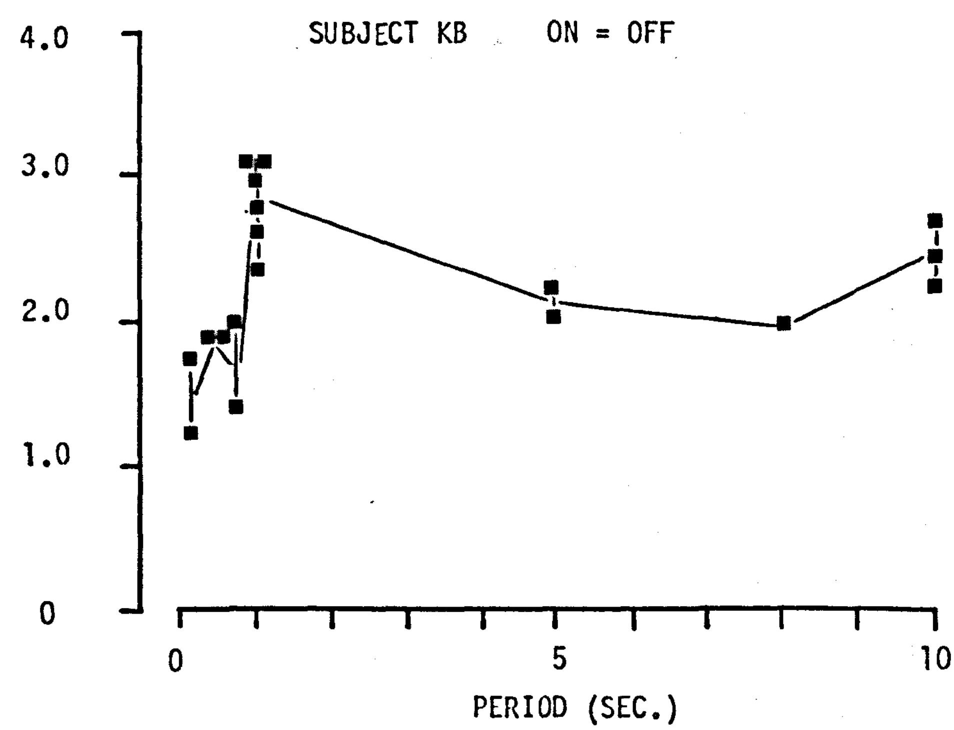


FIG. 4.22 (a)

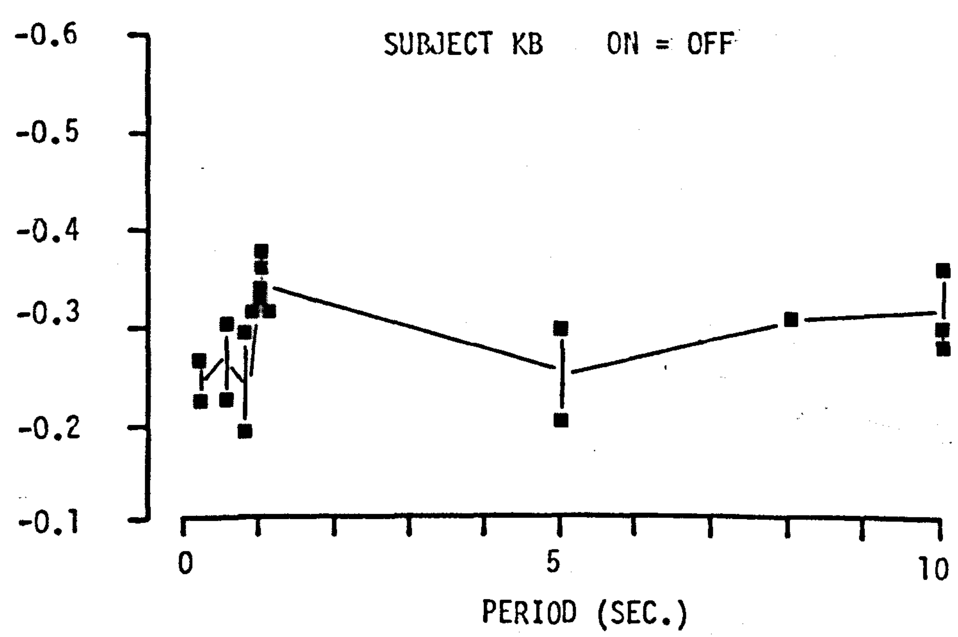


FIG. 4.21(b)

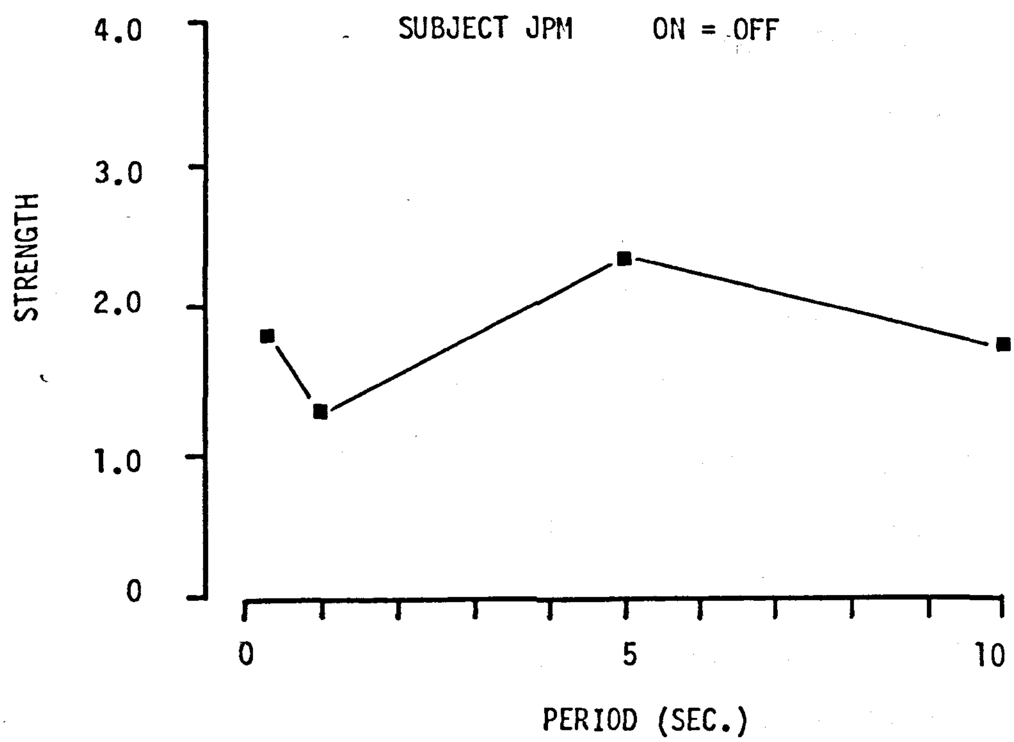
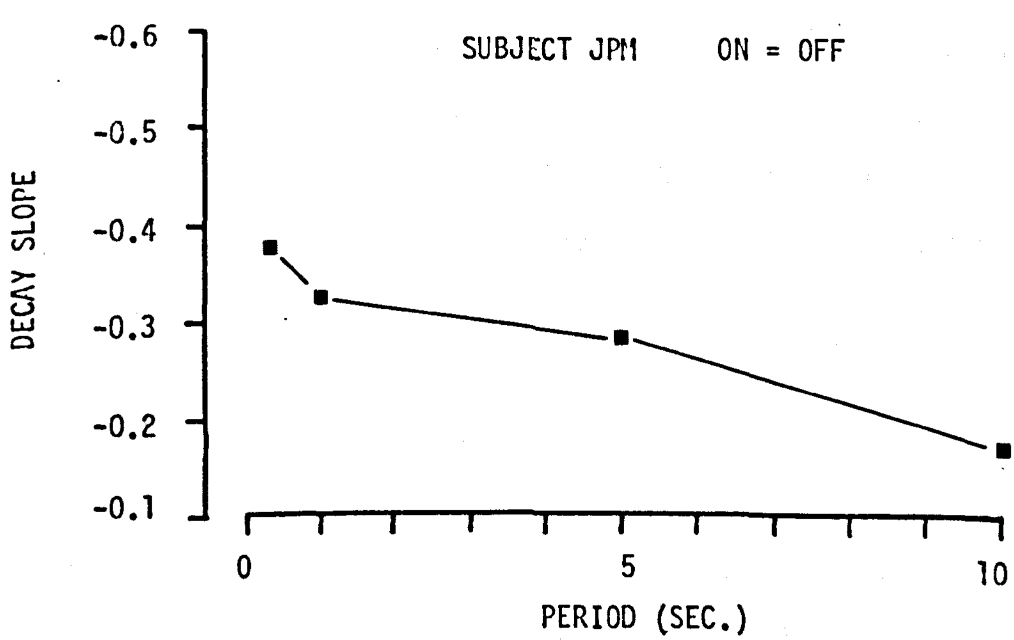


FIG. 4.22(b)



and 'OFF' periods are varied over a wide range of values. The assumption underlying the experiments is that if the ratio itself is the critical parameter, no changes in the strength or decay slope should be observed, though they may differ from series with different ratios. The second group of experiments concerns a particular ratio of 1:10, for a few specific sequences.

4.4.1 Experiments in which the ON:OFF ratio is 1:1

(a) Strength of A/E

The scatter plot shown in Fig. 4.21 indicates very little variation in the mean values for periods less than 1 sec, the overall level being on the low side. There is quite a clear peak in the strength when the periods are 1 sec. When the periods are increased to 5 and 8 sec, the strength drops but is still a little higher than for the shorter periods. There is then a slight rise again when the periods are 10 sec. The results for subject J.P.M. show negligible change throughout the range.

(b) Decay Slope

Fig. 4.22 shows that the changes in the decay slope roughly mimic the changes in strength, with a peak occurring at 1 sec. periods. The graphs of results in Appendix G show that all are nearly linear on log-log co-ordinates. There are no clear trends in the results of subject J.P.M.

4.4.2 Experiments in which a 1:10 ratio is used

Results discussed both in this section and the chapter on the exploratory experiments have shown that the decay slope associated with the sequence 1 sec.'ON'/10 sec. 'OFF' tends to be steeper than that

TABLE 4.11

		Subject K.B.		C.M.J.		D.B.		M.Y.	
ON (sec.)	OFF (sec.)	Strength	Decay Slope	S.	D.S.	S.	D.S.	S.	D.S.
1	10	1.0 1.0 1.2	-0.68 -0.58 -0.42	1.0	-0.42	0.9	-0.33	1.1	-0.33
10	100	1.0 0.8 0.9	-0.19 -0.24 -0.29	0.9	-0.22	1.5	-0.21	1.1	-0.17
20	200	1.4	-0.23						

FIG. 4.23(a)

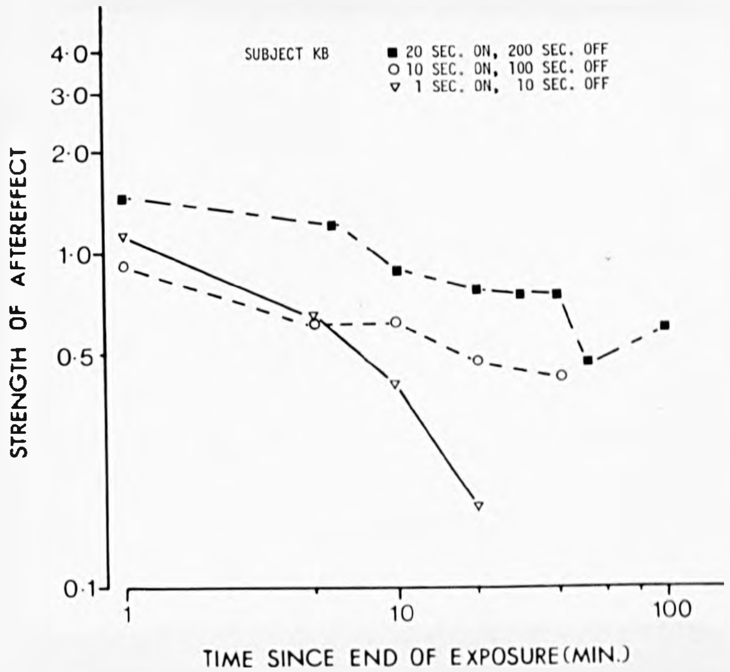


FIG. 4.23 (b)

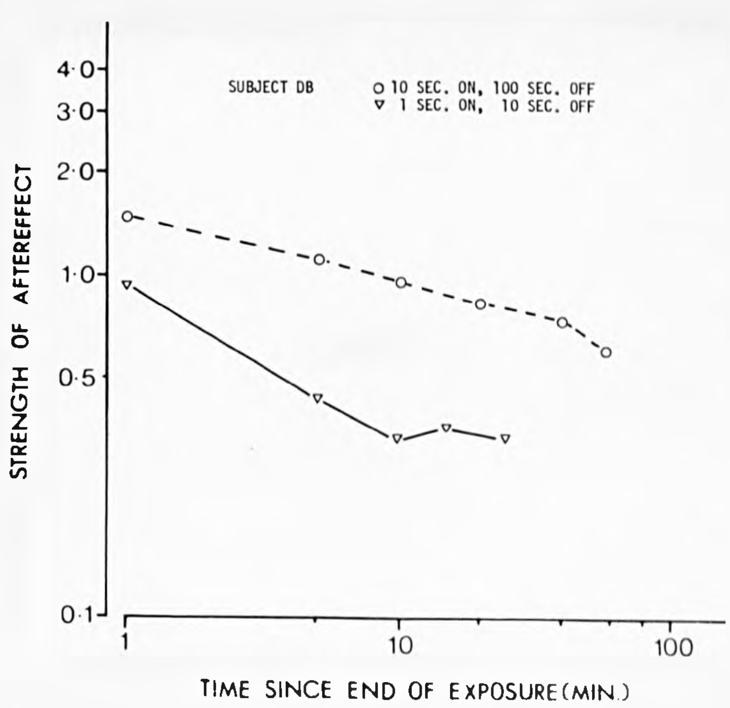


FIG. 4.23 (c)

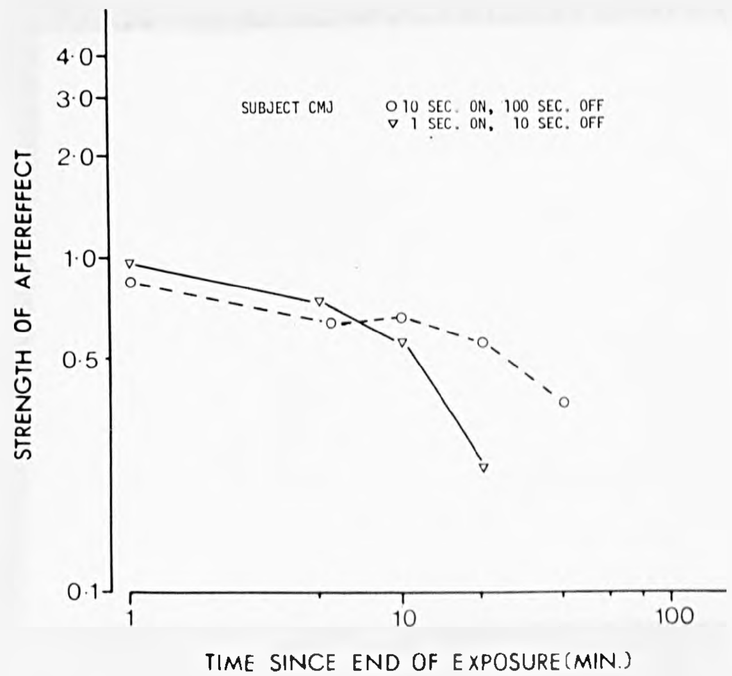
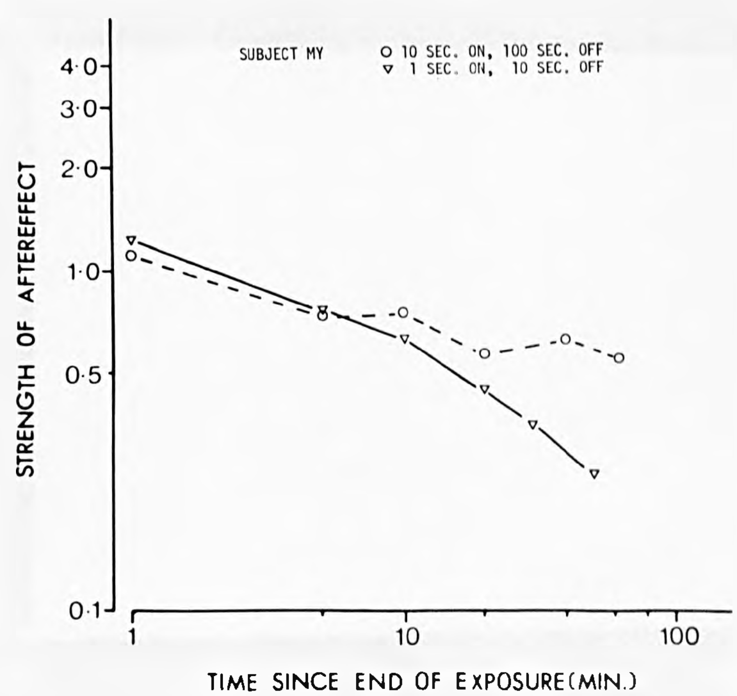


FIG. 4.23 (d)



associated with most other sequences, particular comparison being made with the 10 sec.'ON' and 1 sec.'OFF' sequence. If the critical parameter is the ON:OFF ratio, other sequences with the same ratio but different 'ON' and 'OFF' periods should show the same initial strength and rate of decay. Shorter 'ON' periods with the same ON:OFF ratio yield a smaller strength and steeper rate of decay than the 1 sec.'ON'/10 sec. 'OFF' sequence (see discussion of results for sequence ½ sec.'ON'/5 sec. 'OFF'). The question now is whether temporal sequences with the same 1:10 ratio but with long 'ON' periods will also be associated with a steep decay slope. The results for the two sequences used, together with those for the 1 sec.'ON'/10 sec.'OFF' sequence for comparison, are shown in Table 4.11. It can be seen that the strength is roughly the same for all three sequences. This would seem to implicate the ratio parameter as having an effect on the strength of the A/E. However, the results are very different with respect to the decay slope, the sequence with a 1 sec. 'ON' period having a much steeper rate of decay than the other two. Fig. 4.23 shows that the shape of the decay plot is different for the two groups. The results of these experiments therefore suggest that the rate of decay is not influenced by the ratio of the 'ON' period to the 'OFF' period, but is determined by the particular 'ON' and 'OFF' periods.

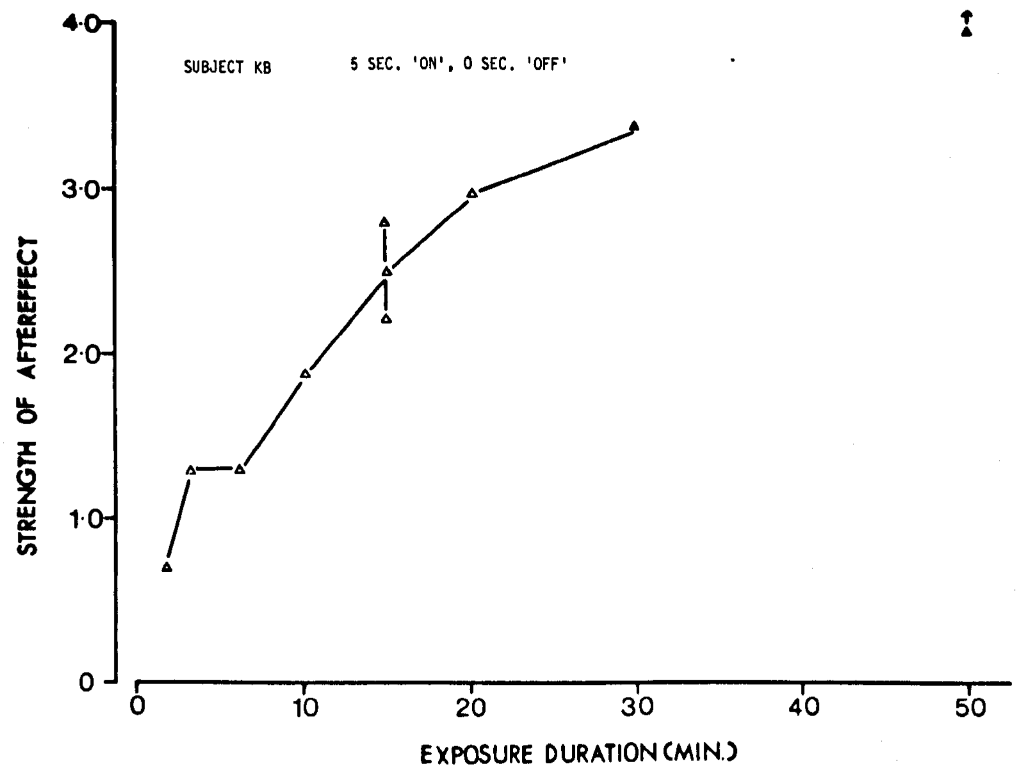
4.5 Duration of adaptation

Two questions underlie this series of experiments. Firstly, for any particular temporal sequence, how does the initial strength of A/E vary with changes in the total duration of adaptation? Assuming that the strength will increase with longer durations, what is the time course of the build-up? Secondly, is there any correlation between strength and rate

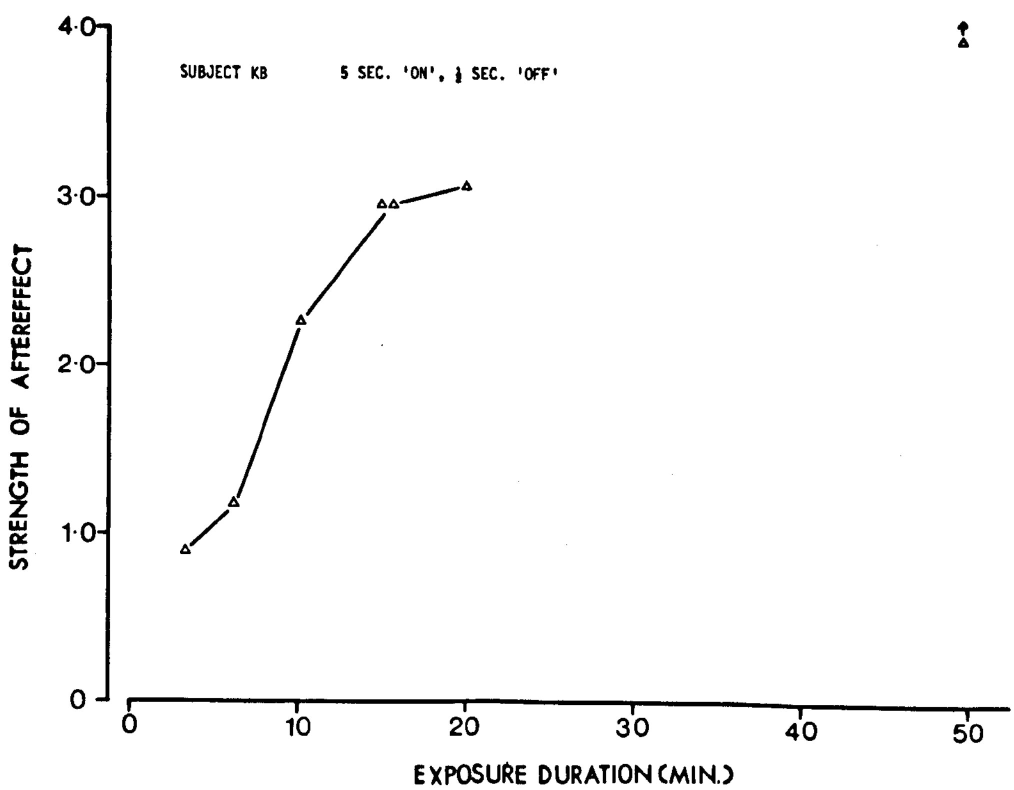
TABLE 4.12 Strength of McCollough A/E related to duration of adaptation for various temporal sequences of stimulation.

Adap'n Duration	½ sec. ON/5 sec. OFF				1 sec. ON/10 sec. OFF				5 sec. ON/0 sec. OFF				5 sec. ON/½ sec. OFF				10 sec. ON/1 sec. OFF				10 sec. ON/10 sec. OFF			
	KB				KB	CMJ	GWB	MY	KB	RM	GWB		KB				KB	GWB	CMJ	MY	KB			
44 secs.																								
88 secs.									0.7_1															
3 min.									1.3_1	0.6_1	0.5_1		0.9_1				1.0_3	0.9_1	0.5_1	1.5				
6 min.					0.7_2		0.3_1		1.3_1				1.2_1				1.6_1	1.5_1			1.1_1			
10 min.									1.9_1		2.6_1		2.3_1								1.4_1			
15 min.	0.6_2				1.0_3	1.0_1	1.3_1		2.5_2	2.1_1			3.0_2				3.2_3	2.4_1	2.1_1	?	2.4_3			
20 min.	1.0_1				1.7_1				3.0_1				3.1_1				3.1_1	3.1_1			3.0_1			
25 min.																								
30 min.	0.8_1				1.1_1		0.6_1		2.4_1									2.7_1						
35 min.																								
40 min.																								
45 min.																								
50 min.	1.7_1				1.5_1	1.5_1	2.0_1		$?_1$				$?_1$					4.1_1						

FIG. 4.24 a

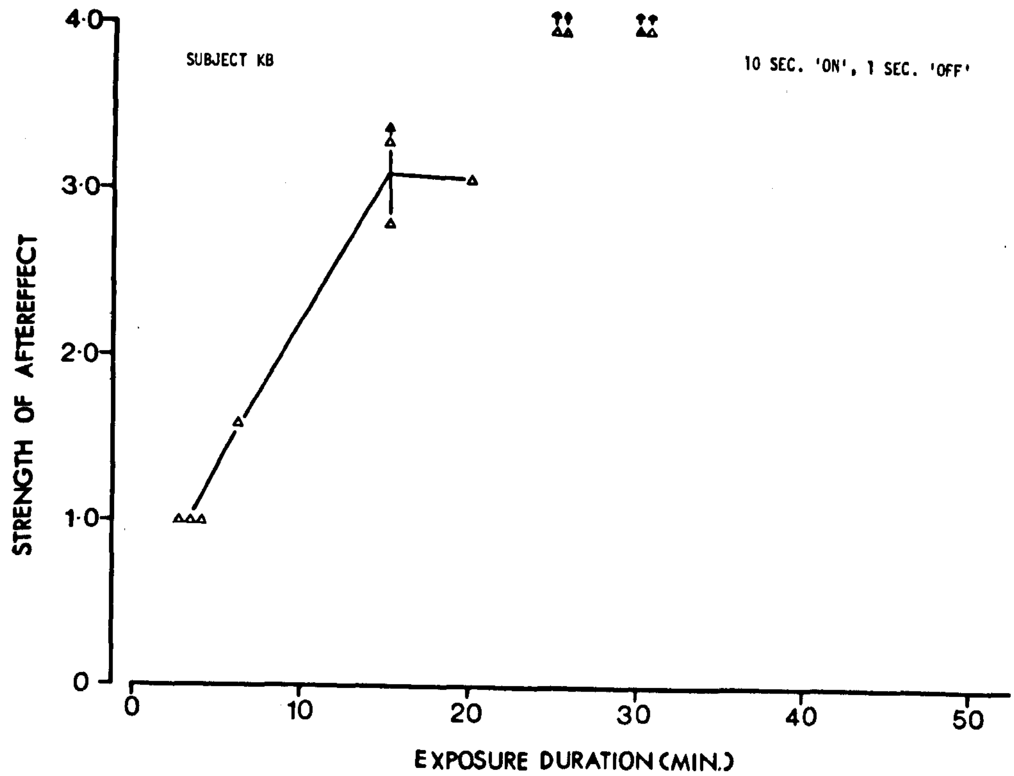


SUBJECT KB
5 SEC. 'ON', 0 SEC. 'OFF'
STRENGTH OF AFTEREFFECT
4·0
3·0
2·0
1·0
0
0
10
20
30
40
50
EXPOSURE DURATION (MIN.)



SUBJECT KB
5 SEC. 'ON', ½ SEC. 'OFF'
STRENGTH OF AFTEREFFECT
4·0
3·0
2·0
1·0
0
0
10
20
30
40
50
EXPOSURE DURATION (MIN.)

FIG. 4.24 a


SUBJECT KB
10 SEC. 'ON', 1 SEC. 'OFF'
STRENGTH OF AFTEREFFECT
4·0
3·0
2·0
1·0
0
0
10
20
30
40
50
EXPOSURE DURATION (MIN.)

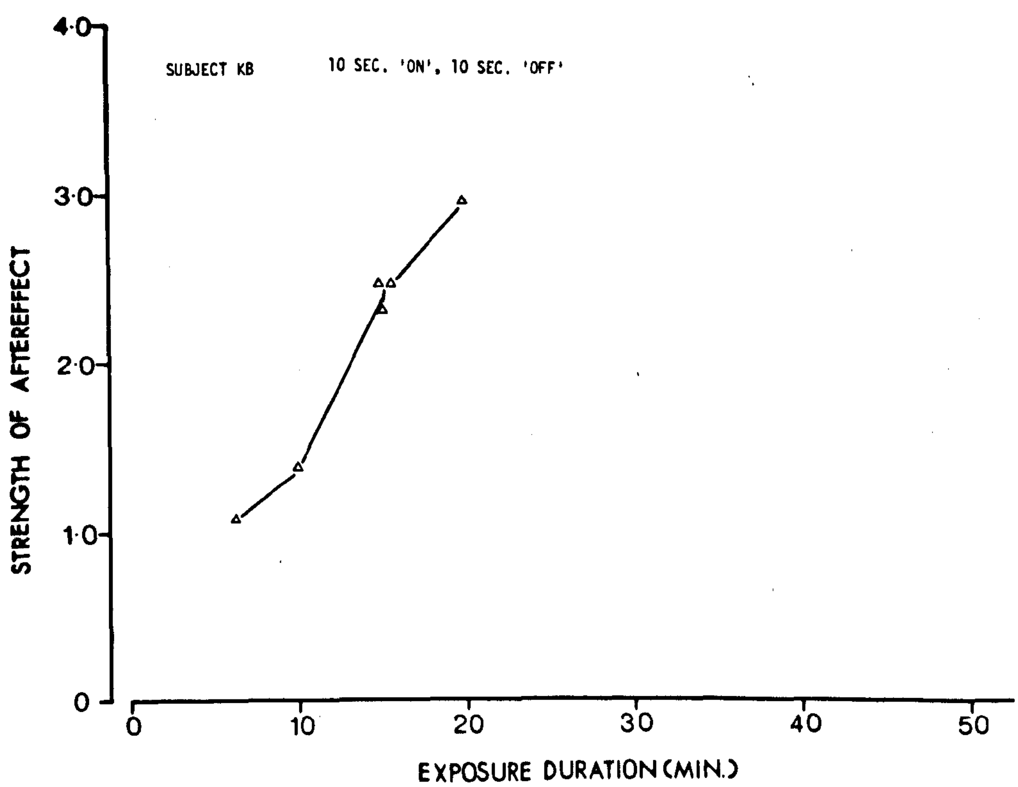
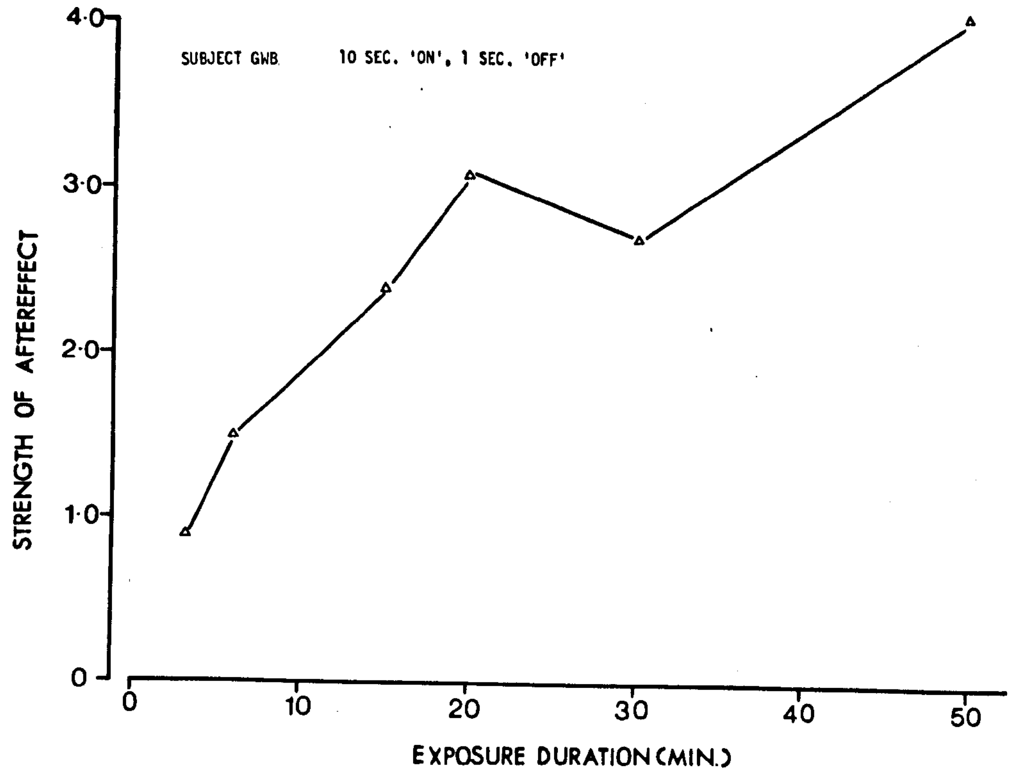

SUBJECT KB
10 SEC. 'ON', 10 SEC. 'OFF'
STRENGTH OF AFTEREFFECT
4·0
3·0
2·0
1·0
0
0
10
20
30
40
50
EXPOSURE DURATION (MIN.)

FIG. 4.24a


SUBJECT GWB
10 SEC. 'ON', 1 SEC. 'OFF'
STRENGTH OF AFTEREFFECT
4·0
3·0
2·0
1·0
0
0
10
20
30
40
50
EXPOSURE DURATION (MIN.)

of decay?

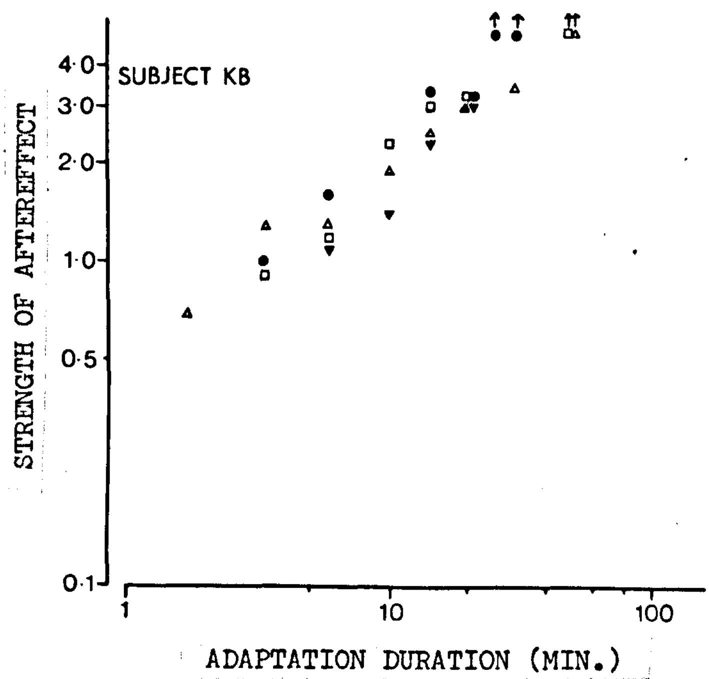
The exploratory experiments indicated that the strength builds up more rapidly at first, and that the increase in strength is not associated with any change in the decay slope when the log. is taken of both time and strength. In order to confirm these points and provide more detailed information, a number of sequences were used. Subject K.B. took part in all experiments, but other subjects were used in two ways; either they took part in a number of experiments on the same sequence or were used simply to compare the results for a short and a relatively long adaptation duration.

4.5.1 Strength of A/E

The results for the whole series for all subjects are summarised in Table 4.12. Comparing the strengths for the shortest and longest adaptation duration for all three subjects, there is clearly an increase in strength for the two sequences with a very short 'ON' period (½ and 1 sec.). For intermediate durations increase in the duration of adaptation does not correlate perfectly with increase in initial strength. The results for the other sequences with a longer 'ON' period do show a more consistent relationship between duration and strength.

Fig. 4.24(a) shows the plot of the build-up in strength with adaptation duration for these sequences. The strength builds up to about 1.0 in the first 3-6 min., and for three of the sequences the plot gives the appearance of a roughly linear, or slightly negatively accelerated, rise to a strength of about 3.0, which is achieved after a 20 min. adaptation. The 5 sec.'ON'/0 sec.'OFF' sequence certainly shows a slowing down in the rate of increase, and this phenomenon is perhaps characteristic

FIG. 4.24 b


SUBJECT KB
STRENGTH OF AFTEREFFECT
4·0
3·0
2·0
1·0
0·5
0·1
1
10
100
ADAPTATION DURATION (MIN.)

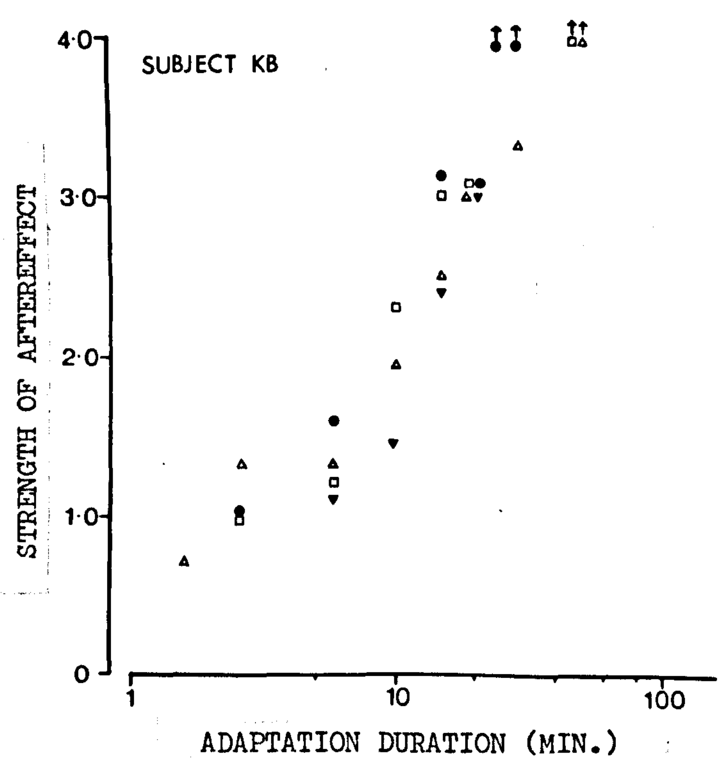

SUBJECT KB
STRENGTH OF AFTEREFFECT
4·0
3·0
2·0
1·0
0
1
10
100
ADAPTATION DURATION (MIN.)

FIG. 4.24 b

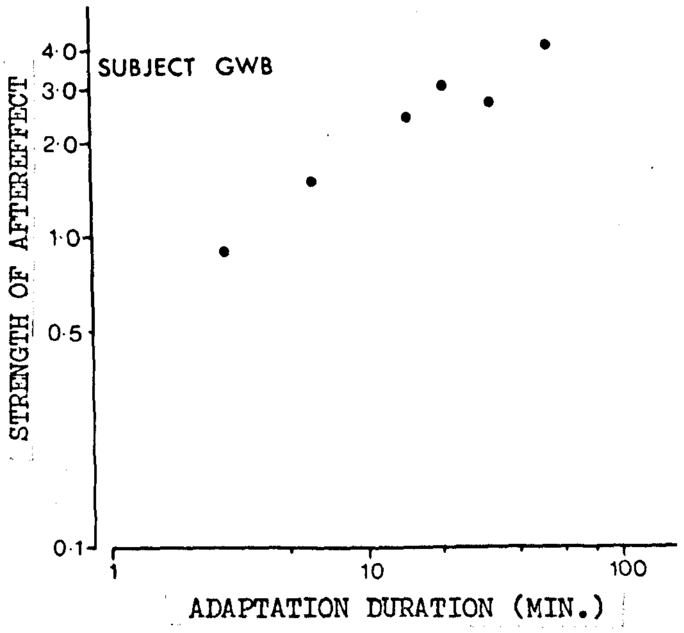
△ 5 SEC. ON, 0 SEC. OFF

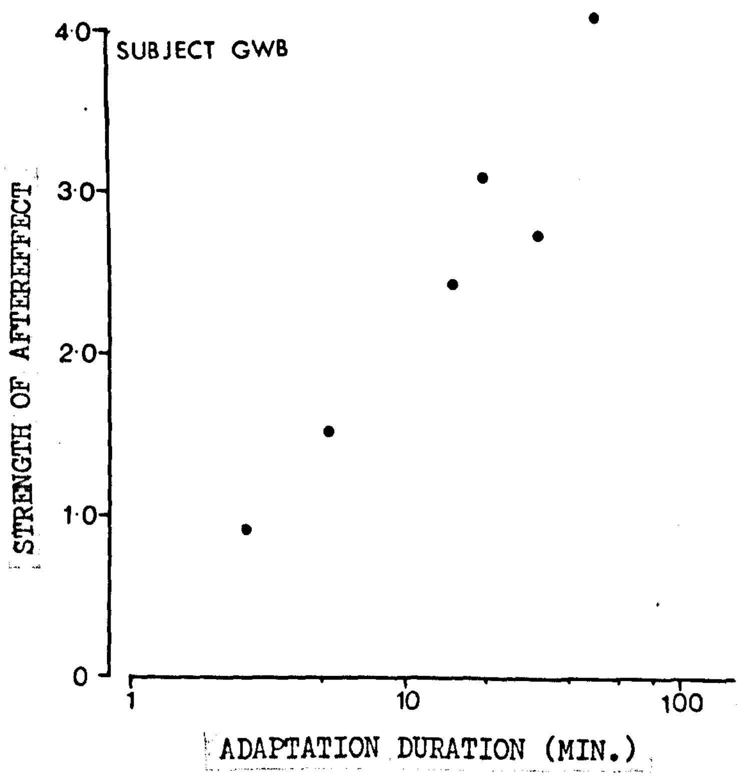
□ 5 SEC. ON, ½ SEC. OFF

● 10 SEC. ON, 1 SEC. OFF

▼ 10 SEC. ON, 10 SEC. OFF

FIG. 4.24 b


SUBJECT GWB
STRENGTH OF AFTEREFFECT
4·0
3·0
2·0
1·0
0·5
0·1
1
10
100
ADAPTATION DURATION (MIN.)


SUBJECT GWB
STRENGTH OF AFTEREFFECT
4·0
3·0
2·0
1·0
0
1
10
100
ADAPTATION DURATION (MIN.)

of the results for subject G.W.B. for the 10 sec.'ON'/1 sec.'OFF' sequence. Changes beyond a strength of about 3.0 are not so clear. For one sequence (10 sec.'ON'/10 sec.'OFF') longer adaptations were not used. For the others, there is clearly an increase but the rate cannot be estimated because the strength goes beyond the measuring range of the apparatus. For the 10 sec.'ON'/1 sec.'OFF' sequence, this has clearly happened with a 25 min exposure, for the 5 sec.'ON'/½ sec.'OFF' it must have happened between 20 and 50 min. and for the 5 sec.'ON'/0 sec.'OFF' sequence at a slightly later point, between 30 and 50 min. Fig. 24(b) shows that for all the results for K.B. a reasonable fit to a straight line is obtained on log-log co-ordinates.

4.5.2 Decay Slope

If there is any correlation between adaptation duration, strength and decay slope one would expect the trend to be consistent across sequences. In the main, this is the case with respect to duration and strength except that there is some variability for sequences in which the 'ON' period is short. Table 4.13 shows that the position is not so clear-cut with respect to duration and decay slope. As the graphs in Appendix H show, the results for some sequences are non-linear on log-log plot. The sequences may be considered in turn:

(i) ½ sec.'ON'/5 sec.'OFF. Subject K.B.: There are too few data points for the 15 min.adaptation to calculate the decay slope. Calculated delay slopes for the other three results are fairly similar, with the 50 min. period having a slightly steeper slope. As the Appendix figures show, the decay for all three results is non-linear on log-log plot.

TABLE 4.13: Decay slope of McCollough Effect calculated on log/log values, for various adaptation durations and sequences.

Adap'n Duration	½ sec. ON/5 sec. OFF				1 sec. ON/10 sec. OFF				5 sec. ON/0 sec. OFF				5 sec. ON/½ sec. OFF				10 sec. ON/1 sec. OFF				10 sec. ON/10 sec. OFF			
	KB				KB	CMJ	GWB	MY	KB	RM	GWB		KB				KB	GWB	CMJ	MY	KB			
44 sec.																								
88 sec.									0.22															
3 min.									0.20_1		0.12_1		0.21_1				0.25_3	0.16_1	0.10_1	-0.15_2				
6 min.					0.97_2		0.97_1		0.21_1				0.36_1				0.21_1	0.23_1			0.44_1			
10 min.									0.26_1		0.24_1		0.26_1								0.50_1			
15 min.	X_2				0.56_3	0.42_1	0.43_1		0.21_2	-0.14_1			0.30_2				0.26_3	0.29_1	0.15_1	-0.36	0.30_1			
20 min.	0.44_1				0.50_1				0.24_1				0.28_1				0.25_1	0.27_1			0.25_1			
25 min.																	0.40_2							
30 min.	0.43_1				0.41_1		0.70_1		0.25_1								0.47_2	0.24_1						
35 min.																								
40 min.																								
45 min.																								
50 min.	0.50_1				0.32_1	0.55_1	0.54_1		0.60_1				0.60_1					0.33_1						

(ii) 1 sec.'ON'/10 sec. 'OFF'. Subject K.B.: The calculated decay slope becomes progressively less steep as the duration of adaptation is lengthened - that is, there is a clear negative correlation between the two measures. However, there is no such clear correlation with the changes in strength as can be seen by comparing the values in Tables 4.12 and 4.13. The decay for the 15 min. adaptation is non-linear on log-log plot and progressively longer durations seem to have the effect of "holding up" the later data points. The results for the 50 min. adaptation show a reasonable fit to a straight line. Other subjects: Results for subject G.W.B. show considerable variability, though the problem here as with other results so far discussed is that some calculated decay slopes are based on very few readings and are therefore not very meaningful. For C.M.J. the decay slope for the 50 min. duration is higher than for the 15 min., which is a change in the opposite direction to that for K.B. Both subjects show either a curve to the data plot or a distinct "drooping" of the later points. The plot for C.M.J. does not "straighten out" in the same way as that for K.B.

(iii) 5 sec. 'ON'/0 sec. 'OFF'. Subject K.B.: There is no systematic change in the calculated decay slope with lengthening of the adaptation duration, though there is a progressive rise in strength. For the 50 min. adaptation, the calculated decay slope is clearly steeper than that for any of the other results of this series. Statistical analysis of the results of the exploratory experiments suggested that for the first reading estimated values are higher than the measured strength, indicating that there may be a curve to the early part of the plot. Calculations based on results with the first data point at 5 or 10 min. are likely to result in a steeper decay slope. Nevertheless, when all the results for this sequence are re-analysed based on a first reading at 10 min. the calculated decay slope for the 50 min. adaptation is still steeper than any of the others.

Other subjects: There are no consistent trends across subjects associated with increase in the adaptation duration.

(iv) 5 sec. 'ON'/½ sec. 'OFF'. Subject K.B.: There is no systematic change in the decay slope with lengthening of the adaptation duration, even though there is a clear positive correlation between strength and duration. The shortest durations have a curved shape to the plot or a "drooping" of the last point but the others show a reasonable fit to a straight line. The 50 min. duration is again associated with a steeper decay line.

(v) 10 sec. 'ON'/1 sec. 'OFF'. Subject K.B.: The calculated decay slopes are fairly similar for four of the durations, and there is no suggestion of non-linearity of decay on log-log plot. The results for the 25 and 30 min. periods show a steeper rate of decay.

Other subjects: All three subjects show a shallower rate of decay following the 3 min. adaptation. Subjects G.W.B. and C.M.J. show no clear change in the calculated decay slope associated with longer adaptations. M.Y. shows a much steeper rate of decay when the adaptation is lengthened to 15 min.

(vi) 10 sec. 'ON'/10 sec. 'OFF'. Subject K.B. The decay slopes are higher for the two shortest durations and the decay is non-linear on log-log plot. Once again, lengthening the exposure duration seems to have the effect of "holding up" the later points. The plots for the longer adaptation periods show a reasonable fit to a straight line.

The occurrence of a non-linear decay on log-log co-ordinates is an interesting problem because it is not observed for all sequences even for the shortest exposure durations. It is quite clear that there is no consistent relationship with either a particular initial strength or exposure duration. It may be that there are systematic differences between sequences with respect to the point at which the decay becomes non-linear. More extreme exposure conditions may have to be imposed on some occasions before the non-linearity becomes apparent.

Finally, these results were plotted on linear-log co-ordinates but this did not provide a better description of the time course of the decay.

4.5.3 Summary

In summary, the following points may be made regarding this series of experiments. (1) With relatively short 'ON' periods, no systematic change in strength appears as the adaptation duration is increased. (2) With longer 'ON' periods there is a good positive correlation between strength and adaptation duration. The build-up is approximately linear on log-log co-ordinates. (3) There is no clear correlation between strength and calculated decay slope. (4) Very strong A/E tend to be associated with a steeper decay slope. Decay is approximately linear on log-log co-ordinates. (5) Short exposure durations and/or weak A/E are sometimes associated with a steeper calculated decay slope, the decay being non-linear on log-log co-ordinates. This non-linearity is not consistently related to either strength or adaptation duration.

4.6 Some general comments regarding strength of the A/E

4.6.1 Strength and decay slope

Earlier it was shown that certain temporal stimulus sequences are

TABLE 4.14 Decay Slopes associated with various ranges of A/E strength (Various Adaptation Durations)

STRENGTH RANGE	INITIAL STRENGTH (MEAN)	DECAY SLOPE (MEAN)	TEMPORAL SEQUENCE OF STIMULATION
≤ 1.5	0.6	?	½ sec. ON/5 sec. OFF
	1.0	-0.44	½ sec. ON/5 sec. OFF
	0.8	-0.43	½ sec. ON/5 sec. OFF
	0.7	-0.97	1 sec. ON/10 sec. OFF
	1.0	-0.56	1 sec. ON/10 sec. OFF
	1.1	-0.41	1 sec. ON/10 sec. OFF
	1.5	-0.32	1 sec. ON/10 sec. OFF
	0.7	-0.22	5 sec. ON/0 sec. OFF
	1.3	-0.20	5 sec. ON/0 sec. OFF
	1.3	-0.21	5 sec. ON/0 sec. OFF
	0.9	-0.31	5 sec. ON/½ sec. OFF
	1.2	-0.36	5 sec. ON/½ sec. OFF
	1.0	-0.25	10 sec. ON/1 sec. OFF
	1.1	-0.44	10 sec. ON/10 sec. OFF
	1.4	-0.50	10 sec. ON/10 sec. OFF
1.6-2.5	1.7	-0.50	½ sec. ON/5 sec. OFF
	1.7	-0.56	1 sec. ON/10 sec. OFF
	1.9	-0.26	5 sec. ON/0 sec. OFF
	2.5	-0.21	5 sec. ON/0 sec. OFF
	2.3	-0.25	5 sec. ON/½ sec. OFF
	1.6	-0.21	10 sec. ON/1 sec. OFF
	2.4	-0.30	10 sec. ON/10 sec. OFF
≥ 2.6	3.0	-0.24	5 sec. ON/0 sec. OFF
	3.0	-0.25	5 sec. ON/0 sec. OFF
	3.0	-0.30	5 sec. ON/½ sec. OFF
	3.1	-0.28	5 sec. ON/½ sec. OFF
	3.2	-0.26	10 sec. ON/1 sec. OFF
	3.1	-0.25	10 sec. ON/1 sec. OFF
	3.0	-0.25	10 sec. ON/10 sec. OFF

associated with an unusually steep decay slope. These sequences also tend to be associated with an initial strength which is quite low. The specific question is whether these weak A/E are always associated with an unusually steep rate of decay. It is important to clarify this point because a high correlation between the two phenomena could be interpreted as evidence for a relationship between the two measures, or else for the existence of a "threshold level" - some A/E strength below which the measuring procedure becomes non-linear.

The conclusion from the analysis in the previous section was that there is no systematic relationship between particular initial strengths and decay slope. As Table 4.14 shows, any particular A/E strength may be associated with any decay slope. This table shows the results of all the experiments concerned with adaptation duration. For purposes of analysis, these results are grouped into three strength ranges. With reference to the lowest range of strength from 0.6-1.5, the range of values for the decay slope extend from -0.20 to -0.97. The mean strength of 1.0, for example, on one occasion has a decay slope of -0.44 associated with it, on another -0.56 and finally one of -0.25.

A similar form of analysis can be carried out on the main body of results of experiments in which the 'ON' and 'OFF' parameters were the independent variables. The results are presented in Table 4.15. All ranges of strength are represented by decay slopes of high and of low value. With respect to the lowest range, an A/E strength of 1.4, for example, occurs on four occasions with decay slope of -0.22, -0.41, -0.29 and -0.23. Moreover, only for certain of the sequences and durations are weak A/E associated with non-linearity of the decay on log-log co-ordinates. Fig. 4.23 may be referred to again, as this shows that sequences having the

TABLE 4.15 Decay Slopes associated with various ranges of A/E strength (Constant Adaptation Duration)

STRENGTH RANGE	INITIAL STRENGTH (MEAN	DECAY SLOPE (MEAN)	TEMPORAL SEQUENCE OF STIMULATION
≤ 1.5	1.4	-0.22	¼ sec. ON/0 sec. OFF
	1.5	-0.25	½ sec. ON/0 sec. OFF
	1.0	-0.37	½ sec. ON/1 sec. OFF
	0.6	?	½ sec. ON/5 sec. OFF
	0.5	?	½ sec. ON/10 sec. OFF
	1.3	-0.42	1 sec. ON/5 sec. OFF
	1.0	-0.56	1 sec. ON/10 sec. OFF
	1.2	-0.41	2 sec. ON/10 sec. OFF
	1.4	-0.41	3 sec. ON/10 sec. OFF
	1.4	-0.29	4 sec. ON/10 sec. OFF
	0.9	-0.24	10 sec. ON/100 sec. OFF
	1.4	-0.23	20 sec. ON/200 sec. OFF
1.6-2.5	1.9	-0.22	½ sec. ON/0 sec. OFF
	1.9	-0.26	½ sec. ON/½ sec. OFF
	2.0	-0.23	¾ sec. ON/0 sec. OFF
	1.7	-0.24	¾ sec. ON/¾ sec. OFF
	2.3	-0.24	1 sec. ON/0 sec. OFF
	1.7	-0.31	1 sec. ON/½ sec. OFF
	1.8	-0.47	2 sec. ON/5 sec. OFF
	2.5	-0.21	5 sec. ON/0 sec. OFF
	2.1	-0.26	5 sec. ON/2 sec. OFF
	2.1	-0.25	5 sec. ON/5 sec. OFF
	1.9	-0.30	7 sec. ON/½ sec. OFF
	2.5	-0.32	7 sec. ON/1 sec. OFF
	2.1	-0.28	8 sec. ON/0 sec. OFF
	2.4	-0.19	8 sec. ON/½ sec. OFF
	2.5	-0.30	8 sec. ON/1 sec. OFF
	2.0	-0.30	8 sec. ON/8 sec. OFF
	2.3	-0.21	9 sec. ON/1 sec. OFF
	1.8	-0.21	10 sec. ON/2 sec. OFF
	2.1	-0.28	10 sec. ON/5 sec. OFF
	2.4	-0.30	10 sec. ON/10 sec. OFF
	1.6	-0.27	5 sec. ON/10 sec. OFF
≥ 2.6	2.8	-0.33	1 sec. ON/1 sec. OFF
	3.3	-0.35	4 sec. ON/1 sec. OFF
	2.7	-0.29	4 sec. ON/2 sec. OFF
	3.0	-0.30	5 sec. ON/½ sec. OFF
	3.0	-0.31	5 sec. ON/1 sec. OFF
	2.8	-0.23	10 sec. ON/0 sec. OFF
	3.1	-0.26	10 sec. ON/½ sec. OFF
	3.2	-0.26	10 sec. ON/1 sec. OFF

same ON:OFF ratio and similar initial strengths are associated with different decay characteristics. We may therefore conclude that over a wide range there is no correlation between initial strength and decay slope.

4.6.2 Strength and temporal sequence

Table 4.16 is presented by way of final summary. A number of points may be made. Firstly, when the 'ON' period is shorter than the 'OFF' period, lengthening the 'ON' is associated with an increase in strength. Secondly, for any particular 'ON' period, strength seems to peak with an 'OFF' period of about 1 sec. Thirdly, provided that the 'ON' is longer than the 'OFF' the system can tolerate a wide range of increase in the length of the 'OFF' period (and therefore a reduction in the total time of exposure) without any adverse effect on the strength of the A/E. For example, for the 10 sec. 'ON' series of experiments, increase in the length of the 'OFF' period from 0 sec. to 10 sec. was not accompanied by a systematic reduction in strength.

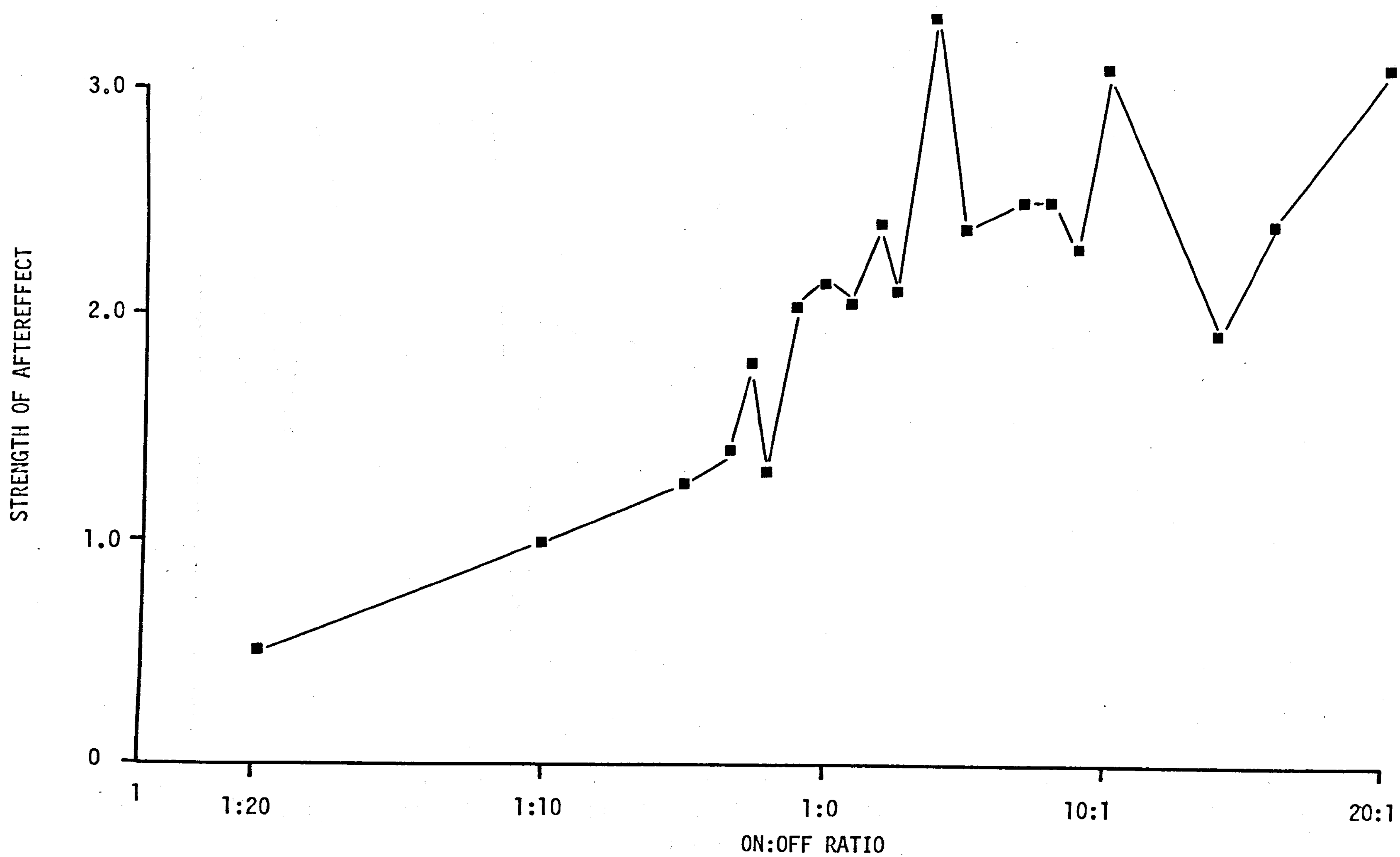
Figure 4.25 is a plot of the mean values, ignoring scatter. Although the scatter is quite wide around many points, this does make clear that there is an approximately linear increase in strength as the 'ON' is lengthened to a ratio approaching 1:1. Beyond that, there is no systematic change in strength with further change in the ratio.

Finally, we may consider the question of the role of the cycle duration. The conclusion drawn from the exploratory experiments was that there is no correlation between changes in strength and variation in the length of the cycle duration. The data from this main part of the study may now be analysed in relation to this point. Figure 4.26 is a plot of mean strength against cycle duration. This confirms that the

TABLE 4.16 Subject KB Strength of A/E 1 min. after end of adaptation period

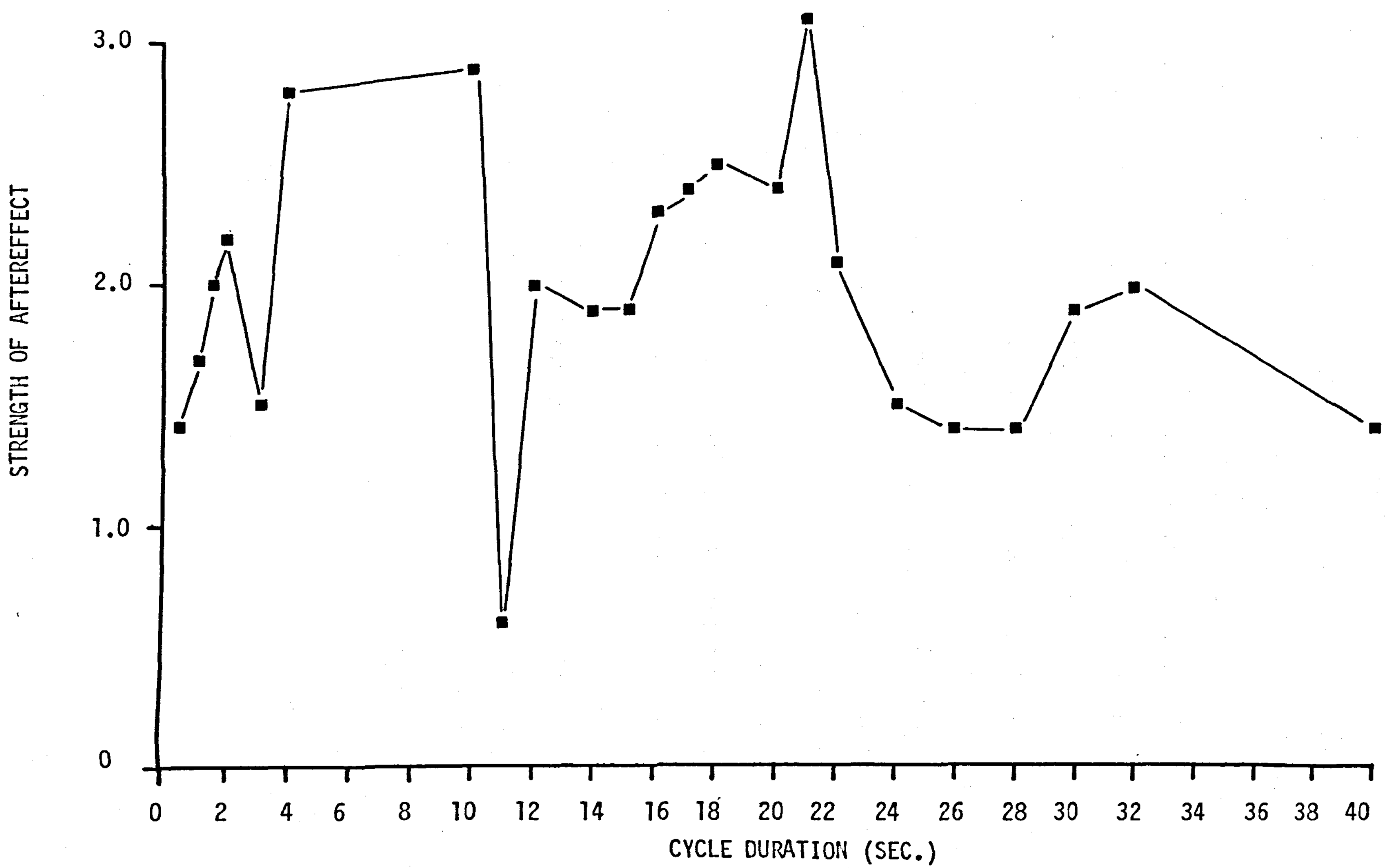
'OFF' PERIOD (sec.)		'ON' PERIOD (sec.)													
		¼	½	¾	1	2	3	4	5	6	7	8	9	10	20
0		1.4_3	1.9_2	2.0_3	2.3_2				2.5_2			2.1_2		2.8_3	
¼		1.5_2													
½			1.9_2		1.7_1				3.0_2		1.9_1	2.4_2		3.1_1	
¾				1.7_2											
1			1.0_1		2.8_6			3.3_1	3.0_2		2.5_2	2.5_3	2.3_1	3.2_3	
2								2.7_1	2.1_2					1.8_1	
3															
4															
5			0.6_2		1.3_2	1.8_1			2.1_2					2.1_2	
6															
7															
8												2.0_1			
9															
10			0.5_1		1.1_3	1.2_2	1.4_2	1.4_2	1.6_2					2.4_3	
100														0.9_3	
200															1.4

FIG. 4.25



STRENGTH OF AFTEREFFECT
3.0
2.0
1.0
0
1
1:20
1:10
1:0
10:1
20:1
ON:OFF RATIO

FIG. 4.26



STRENGTH OF AFTEREFFECT
3.0
2.0
1.0
0
0 2 4 6 8 10 12 14 16 18 20 22 24 26 28 30 32 34 36 38 40
CYCLE DURATION (SEC.)

two measures are uncorrelated.

4.7 Some general comments regarding the decay slope

Table 4.17 is a summary of results showing how the decay slope varies with the temporal parameters of stimulation. Previous discussion has made clear that there is no simple correlation with the A/E strength. The steepest calculated decay slopes tend to occur with temporal sequences composed of a short 'ON' period and a relatively long 'OFF'. The 'ON' period itself is not critical since none of the sequences with a 0 sec. 'OFF' period are associated with these unusually steep decay slopes. Equally, a long 'OFF' period is not itself critical since the sequences with 100 and 200 sec. 'OFF' are associated with fairly shallow decay slopes. These decay slopes are associated with particular combinations of 'ON' and 'OFF' periods. These sequences tend to be associated with a decay which is non-linear when plotted on log-log co-ordinates. Decay may also become non-linear on log-log plot if the adaptation duration is made sufficiently short, whatever the temporal parameters of the stimulus sequence.

Equally, there are other occasions on which an unusually steep decay is observed with a linear decay on log-log plot. 'OFF' periods of ½ or 1 sec. tend to have steeper decay slopes, whatever the 'ON' period. Very long adaptation durations are also associated with steeper decay slopes.

TABLE 4.17

'OFF' PERIOD (sec.)	'ON' PERIOD (sec.)		¼	½	¾	1	2	3	4	5	6	7	8	9	10	20
	0		-0.22_3	-0.22_2	-0.23_3	-0.24_2				-0.21_2			-0.28_2		-0.23_3	
	¼		-0.25_2													
	½			-0.26_2		-0.31_1				-0.30_2		-0.30_1	-0.19_2		-0.26_1	
	¾				-0.24_2											
	1			-0.37_1		-0.33_6			-0.35_1	-0.31_2		-0.32_2	-0.30_3	-0.21_1	-0.26_3	
	2								-0.29_1	-0.26_2					-0.21_1	
	3															
	4															
	5			X		-0.42_2	-0.47_1			-0.25_2					-0.28_2	
	6															
	7															
	8												-0.30_1			
	9															
	10			X		-0.56_3	-0.41_2	-0.41_2	-0.29_2	-0.27_2					-0.30_3	
	100														-0.24_3	
	200															-0.23_1

4.8 Summary

1. The discrete temporal parameters of the stimulation sequence exert an influence on both initial strength and decay rate of the A/E.
2. For a constant 'OFF' period and total adaptation duration, increase in the length of the 'ON' period from ¼ sec. to about 1 sec. is associated with a linear increase in strength of A/E. The most rapid rate of increase in strength occurs over this range of 'ON' periods, but the rate also depends on the length of the associated 'OFF' period. Shorter 'OFF' periods are associated with a more rapid rate of increase.
3. Lengthening the 'ON' period beyond 1 sec. for a constant adaptation duration may be associated with further systematic changes in initial strength. The critical factor appears to be the relative lengths of the 'ON' and 'OFF' periods. Lengthening the 'ON' period beyond 1 sec. is associated with a further systematic increase in initial strength, provided the length of the 'ON' period does not exceed that of the 'OFF'. The rate of increase is less steep than over the range ¼-1 sec. 'ON'. No systematic changes in strength are observed once the 'ON' period exceeds the length of the 'OFF'.
4. For the 'ON' periods studied for one subject, increasing the length of the 'OFF' from 0 to 1 sec. is associated with a rise in the strength of the A/E. This increase in strength may occur even though lengthening the 'OFF' results in a substantial decrease in the total duration of exposure to the adapting patterns. Further increase in the 'OFF' period to 2 sec. is accompanied by a sharp decrease in A/E strength. Changes in strength are less certain for further lengthening of the 'OFF' period up to the point at which the 'ON' and 'OFF' become equal. Beyond that, strength decreases approximately linearly with increase in the length of the 'OFF'. For all 'ON' periods studied,

therefore, peak strength occurs when the 'OFF' is 1 sec. There may be systematic differences between subjects for the 'OFF' period giving peak strength.

5. Although there is some variability for sequences with a short 'ON' period and relatively long 'OFF', A/E strength increases with the duration of adaptation. Increase in strength is approximately linearly related to duration on a log-log plot.

6. There is no correlation between initial strength and decay slope on such a plot. Decay slope does vary systematically with the parameters of the temporal sequence of stimulation.

7. Overall, the shallowest decay slopes are associated with the series having a 0 sec. 'OFF' period. For all 'ON' periods, lengthening the 'OFF' from 0 to 1 sec. is associated with an increase in the value of the calculated decay slope. For the three 'ON' periods studied (4, 5 and 10 sec.), lengthening the 'OFF' from 2 to 3 sec. is associated with a sharp decrease in the calculated decay slope. It is not clear whether or not there are systematic differences between subjects in the point of transition.

8. For 'ON' periods of 4 sec. or longer, lengthening the 'OFF' beyond 2 sec. is associated with very little change in the decay slope. Decay is approximately linear on log-log co-ordinates.

9. When the 'ON' period is less than 4 sec., the calculated decay slope increases with lengthening of the 'OFF' period. For relatively long 'OFF' periods (5 or 10 sec.), these calculated decay slopes tend to be associated with a non-linear decay on log-log plot. Equally, for these long 'OFF' periods, lengthening the 'ON' from ½ to 4 sec. is associated with decrease in the calculated slope. For the shortest 'ON' periods, decay is non-linear on log-log plot

but approximately linear on linear-log co-ordinates. There is a point of transition occurring with 'ON' periods in the range 2-4 sec. (perhaps sharply defined between 3 and 4 sec.), when decay becomes linear on log-log co-ordinates.

10. These changes in decay characteristics do not occur over this range of 'ON' periods when the associated 'OFF' period is relatively short (0 to 1 sec.). Moreover, although the associated strength tends to be small there is no simple correlation with strength since some other sequences have similar initial strengths but do not show any evidence of steep decay slopes or non-linear decay on log-log co-ordinates.

11. When the log is taken of both time and strength values, calculated decay slope may also vary with variation in the duration of adaptation, for a given temporal sequence of stimulation. For the shortest exposure durations, calculated decay slopes tended to be unusually steep, but decay was non-linear on a log-log plot. Calculated decay slope became less steep and decay approximately linear on log-log plot for intermediate exposure durations. Extremely long exposures (e.g. of 30 min. or 50 min.) on occasion gave rise to unusually steep decay slopes and on these occasions decay was approximately linear on a log-log plot.

CHAPTER 5: EFFECT OF INTERPOSING A PERIOD OF DIFFUSE ACHROMATIC ILLUMINATION INTO THE INTERSTIMULUS INTERVAL

In mid 1974 MacKay and MacKay showed that if the eyes are totally occluded immediately after adaptation no decay of the A/E occurs, but a normal rate of decay is observed when the eyes are subsequently uncovered. Post adaptation exposure to only diffuse illumination does not arrest the decay. The implication is that visual stimulation is essential for triggering the decay process. This raises the question whether a period of diffuse achromatic illumination inserted into the interstimulus interval will be associated with a reduced strength of A/E relative to equivalent experiments with a totally dark interstimulus period. The main questions at this stage concerned the effect on the strength, but the possibility also existed that white illumination in the adaptation period would cause an abnormal decay process, since there would be an alternation of build-up and then decay as one sort of stimulation induces the A/E and the other initiates decay. The duration of the achromatic illumination, and the temporal location relative to the onset and offset edges of pattern stimulation, were parameters also thought capable of exerting a critical influence.

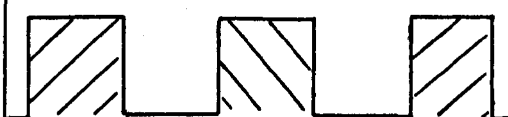
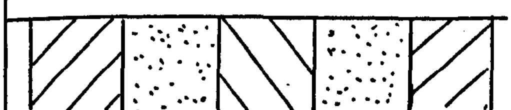
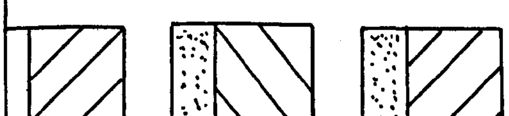
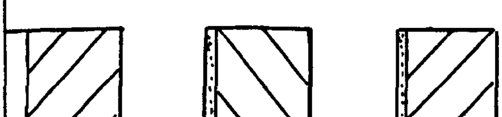
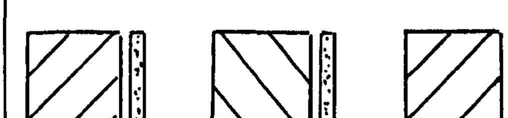
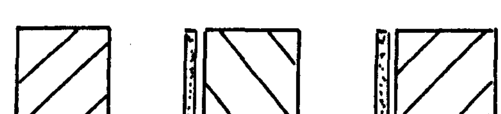
Exploratory experiments were carried out in early 1975, though repeat runs were only carried out later. A temporal sequence with 10 sec. of pattern stimulation and a 10 sec. interstimulus 'OFF' period was used in all experiments at this stage. A sequence with a long 'OFF' period was used because this provided sufficient flexibility for varying both the duration and location of the period of achromatic illumination. Graphs are presented in Appendix I for the results of each individual experiment.

A summary of the results, including calculated decay slopes, is shown in Table 5.1. The first experimental condition simply involved filling the whole of the interstimulus period with diffuse illumination, which would establish whether or not diffuse illumination does have the effect expected. It can be seen that it does. The strength of the associated A/E is reduced by about 25% compared with results when the whole of the interstimulus period is dark, and there is no overlap of the readings between conditions. The calculated decay slopes are slightly shallower but not enough to arouse serious interest, and decay is linear on log-log plot. The next question was whether the amount of the reduction in strength is related to the duration of the period of illumination. Table 5.1 shows that when the period of illumination is reduced to 5 sec., onset being simultaneous with pattern offset, the strength is approximately the same as in the previous experiment. The decay slope is slightly steeper and is identical with that associated with the equivalent sequence with a dark interstimulus period. Decay is linear on log-log co-ordinates. Further reduction of the white period to 1 sec. is associated with another slight decrease in the strength, which is now down by 40% compared with the results when there is no such period. The decay slopes are very similar and decay is linear on log-log plot.

We may conclude from this series of experiments that a period of diffuse achromatic illumination in the interstimulus interval does impede establishment of the A/E. This effect is not linearly related to the duration of the period of illumination, at least for periods of length 1 sec. to 10 sec. A 1 sec. period can be at least as effective as a 10 sec. period.

The next question concerned the importance of the location of the pulse of achromatic illumination. Will the results be the same if the illumination occurs just prior to pattern onset, rather than at pattern

TABLE 5.1

TEMPORAL SEQUENCE		DECAY/ SLOPE		STRENGTH	
		VALUES	MEAN	VALUES	MEAN
	10 SEC. ON 10 SEC. OFF	-0.27 -0.29 -0.35	-0.30	2.5 2.3 2.5	2.4
	10 SEC. ON 10 SEC. ACHROM.	-0.28 -0.22	-0.25	1.9 1.6	1.8
	10 SEC. ON 5 SEC. ACHROM. 5 SEC. OFF	-0.32 -0.30	-0.31	1.7 1.6	1.7
	10 SEC. ON 1 SEC. ACHROM. 9 SEC. OFF	-0.25 -0.28	-0.27	1.3 1.6	1.5
	10 SEC. ON 5 SEC. OFF 5 SEC. ACHROM.	-0.32 -0.31	-0.32	2.2 1.5	1.9
	10 SEC. ON 9 SEC. OFF 1 SEC. ACHROM.	-0.25 -0.28	-0.27	1.3 1.6	1.5
	10 SEC. ON 1 SEC. OFF 1 SEC. ACHROM. 8 SEC. OFF	-0.36 -0.39	-0.38	2.2 2.3	2.3
	10 SEC. ON 8 SEC. OFF 1 SEC. ACHROM. 1 SEC. OFF	-0.35		2.7	

offset? The fifth experiment is similar to the second, but with the second half of the interstimulus period illuminated rather than the first. The strength is very similar to that for conditions 2 and 3. The calculated decay slope is also very similar and decay is linear on log-log plot. Reduction of the stimulation period to 1 sec.(condition 6) is associated with an average strength identical with that for condition 5. This is higher than that for condition 4 in which the 1 sec. pulse occurred at pattern offset. The decay slope is steeper on one occasion than any calculated for previous experiments of this series, and decay is non-linear on log-log co-ordinates. Without the benefit of further repeat experiments it is difficult to attach too much significance to this result.

At this point the conclusion seemed to be that the critical period during which the strength - and perhaps the rate of decay - can be influenced by a period of white illumination is only the 1 sec. immediately after pattern offset or the 1 sec. immediately prior to pattern onset. If it is only this 1 sec. period which is important, separating the period of diffuse illumination from the period of pattern stimulation by 1 sec. of darkness should put the pulse of achromatic stimulation outside the critical time period during which it may exert an impeding influence on the establishment of the A/E. Two further experiments were therefore carried out in which the onset of a 1 sec. pulse of achromatic illumination was delayed by either 1 sec. or 8 sec. relative to pattern offset.

The results (Table 5.1) show that for both there is effectively no reduction in the strength of the A/E compared with condition 1. The decay slopes are a little on the high side but not significantly different from the other results of this series. Decay is approximately linear on log-log plot.

In conclusion, the process of establishment of A/E would seem to be impeded by a short period of achromatic illumination in the interstimulus period. This process of establishment of the effect can only be interfered with immediately prior to or immediately after a period of pattern stimulation. There is limited evidence to suggest that the precise nature of the interference effect may not be identical under the two conditions, but may vary in relation to the location of the pulse.

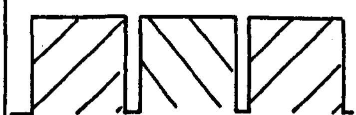
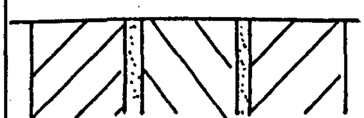
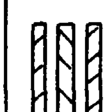
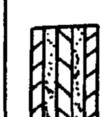
Having established the effect, this project was put into 'cold storage' until more data had been gathered on the influence of temporal parameters of stimulation. It seemed likely that the results of this parametric study would provide important clues in the choice of further critical temporal sequences in relation to studies of the effect of inserting periods of diffuse illumination into the adaptation. Two facts emerged which seemed important for an understanding of the fine time structure of the A/E. Firstly, the establishment of the A/E can be influenced by the length of the 'ON' period. A critical time period in relation to the 'ON' is no more than about 4 sec. and may be less under ideal circumstances. Long 'ON' periods have little if any additional influence. Secondly, A/E strength tends to 'peak' with 'OFF' periods of about 1 sec. When the associated 'ON' period is long, lengthening the 'OFF' period beyond 1 sec. is associated with only a slight decrease in strength. However, when the 'ON' period is short, lengthening the 'OFF' beyond 1 sec. is associated with a substantial reduction in strength and a change in the characteristics of the process of decay. These points influenced the choice of experiments when this project was resumed towards the end of 1975.

The unusually high strength associated with sequences with a 1 sec. dark 'OFF' period are of interest in relation to the finding that establishment of the A/E can be impeded by the inclusion in the temporal sequence of a 1 sec. period of achromatic illumination, provided that this is timed to occur immediately after pattern offset. The next question is how strength and decay slope will be affected when the 1 sec. dark 'OFF' period is replaced by a 1 sec. period of diffuse illumination. Two sequences were chosen to investigate this quickly, one with a long 'ON' period (10 sec.) and the other with a relatively short 'ON' (1 sec.). Strengths and decay slopes associated with these 'ON' periods are similar when the dark 'OFF' period is 1 sec. (see Table 4.16, and Table 4.17).

As Table 5.2 shows, for an 'ON' period of 10 sec. the strength is 2.0 when the interstimulus period is illuminated, compared with 3.2 when it is dark. This is a reduction of 1.2 or a little over 30%. However, the measured strength is slightly higher than that associated with conditions 2-6. The calculated decay slope for one result is similar to that associated with a temporal sequence with a 1 sec. dark 'OFF' period, and decay is linear on log-log co-ordinates (a mains power failure during the course of the repeat experiment prevented following decay over an extended period). When the 'ON' period is 1 sec. however, strength is reduced from 2.8 when the 'OFF' is dark to 1.1, a reduction of more than 50% and the level is much lower than any so far recorded following a sequence which includes a period of achromatic illumination. The decay slope for one result is similar to that characteristic of a sequence with a dark 'OFF' but the other is considerably steeper. As the graphs show, decay is non-linear on log-log plot.

This differential effect related to the length of the 'ON' period raises the question whether the level of reduction will vary in a similar way when the total 'OFF' period is of long rather than short duration. It was

TABLE 5.2

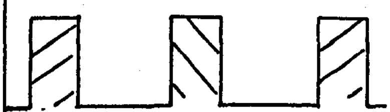
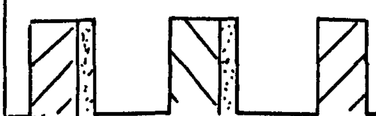
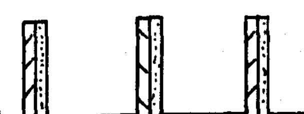
TEMPORAL SEQUENCE		DECAY SLOPE		STRENGTH	
		VALUE	MEAN	VALUES	MEAN
	10 SEC. ON 1 SEC. OFF	-0.29 -0.27 -0.22	-0.26	3.4 2.8 3.3	3.2
	10 SEC. ON 1 SEC. ACHROM.	? -0.23		1.8 2.1	2.0
	1 SEC. ON 1 SEC. OFF	-0.35 -0.31 -0.31 -0.32 -0.37 -0.33	-0.33	3.1 3.1 2.7 2.5 2.6 2.4	2.8
	1 SEC. ON 1 SEC. ACHROM.	-0.55 -0.30	-0.42	1.0 1.1	1.1

therefore thought of interest to use a 10 sec. 'OFF' period, with the first second after pattern offset illuminated and the remaining 9 sec. totally dark. This would provide a convenient standardised 'OFF' sequence, but for the present purposes we have ignored any possible differences of effect related to the location of the 1 sec. pulse. A sequence with a 10 sec. 'ON' period had already been used, and so a rough guide to the nature of the changes could be quickly gained by using sequences with 5 sec. and 1 sec. 'ON' periods. It should be remembered that these three different 'ON' periods are associated with different strengths and decay slopes when the 'OFF' period is constant at 10 sec. and completely dark.

The results for all three sequences are summarised in Table 5.3. (the results for the 10 sec. 'ON' period being repeated for convenience of comparison). When the 'ON' period is 5 sec. the average strength is only a little lower than that associated with the 10 sec. 'ON' period. However, compared with the similar sequence in which the 'OFF' period is totally dark, the reduction is very small - less than 20% compared with about 40% for the longer 'ON' period. When the 'ON' period is further reduced to 1 sec. the associated A/E strength is smaller in comparison with the two other experiments with the same 'OFF' sequence, but the reduction is still about 20% or less relative to the 1 sec. 'ON'/10 sec. dark 'OFF' sequence. The actual difference in strength associated with the introduction of the 1 sec. period of illumination is only about 0.2 and for the 5 sec. 'ON' period it is 0.3, so these two sequences have both the smallest proportional and real reductions in strength.

With respect to the decay of the A/E, the calculated slopes for the 5 sec. 'ON' sequence are very similar to those associated with a 10 sec. 'ON' period and for the equivalent 5 sec. 'ON' with a completely dark 'OFF' period. Decay is linear on log-log co-ordinates. For the 1 sec. 'ON'

TABLE 5.3

TEMPORAL SEQUENCE		DECAY SLOPE		STRENGTH	
		VALUES	MEAN	VALUES	MEAN
	5 SEC. ON 10 SEC. OFF	-0.27 -0.26	-0.27	1.6 1.6	1.6
	5 SEC. ON 1 SEC. ACHROM. 9 SEC. OFF	-0.32 -0.29	-0.31	1.4 1.2	1.3
	1 SEC. ON 10 SEC. OFF	-0.68 -0.58 -0.42	-0.56	1.0 1.0 1.4	1.1
	1 SEC. ON 1 SEC. ACHROM. 9 SEC. OFF	-0.40		0.9	

sequence the decay slope is much steeper and decay is non-linear on log-log co-ordinates, but both these features are characteristic of the equivalent sequence with a completely dark interstimulus period.

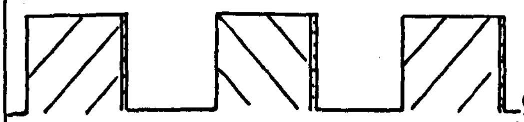
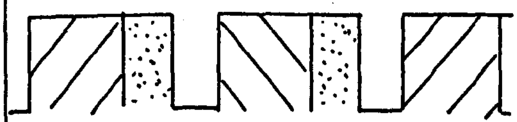
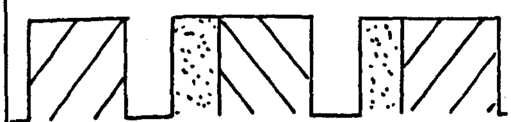
This second series of experiments, in which the 'ON' and 'OFF' periods were each fixed in turn, allowed the effect of a 1 sec. period of achromatic illumination to be assessed in relation to the length of these 'ON' and 'OFF' periods. For the sequences with a 1 sec. white 'OFF' with no period of darkness, it is clear that the strength associated with a 1 sec. 'ON' is much lower and decay slope steeper than the results associated with a 10 sec. 'ON' period. Comparing these results with those associated with equivalent sequences in which the 'OFF' period is completely dark, it is clear that the introduction of a period of illumination has had a greater disruptive effect in the case of the sequence with a 1 sec. 'ON' period - when the 'OFF' was dark the results were similar for the two 'ON' periods, but when the 'OFF' period is illuminated the results are dissimilar. Moreover, decay is non-linear on log-log co-ordinates for the sequence with the short 'ON' period.

When the total 'OFF' period is 10 sec. with a 1 sec. period of achromatic illumination, A/E strength becomes progressively weaker and decay slope steeper as the length of the 'ON' period is reduced. In this respect the results are similar to those already discussed. Comparing these results with those of equivalent sequences with a totally dark 'OFF' period, it is clear that the introduction of a period of illumination has had less of an impeding influence for the sequence with the shorter 'ON' period. This is the opposite effect to that shown in the previously discussed experiments. Decay slopes are similar and decay is non-linear on log-log plot in the case of the 1 sec. 'ON' experiments.

Comparison of results for the same 'ON' period but different 'OFF' sequences may be made, but with more caution. For the experiments employing a long 'ON' period, establishment of the A/E is impeded by about the same amount for both 'OFF' conditions. However, for the experiments with a short 'ON' period, establishment and persistence of the A/E is impeded to a much greater extent for the condition with a short 'OFF' period, results for the long 'OFF' period being very similar to those associated with a completely dark 'OFF'. Moreover, the results for the 1 sec.'ON'/1 sec. 'white' sequence are in all respects very similar to those associated with the 1 sec. 'ON'/10 sec.'OFF' and 1 sec. 'ON'/1 sec. 'white'/9 sec. dark 'OFF' sequences. It would seem that under these circumstances the period of achromatic illumination has an effect similar to that produced by a long period of darkness between successive coloured pattern stimuli. That is, it may serve to isolate in time the successive McCollough stimuli.

In conclusion, three further experiments were carried out to quickly check on whether 1 sec.is the critical period for the diffuse illumination to have an effect, or whether some shorter period will be equally effective (provided that it is strategically placed). The results are presented in Table 5.4. A duration of about 100 msec.is about the shortest that can be used before the energy factor intrudes (Bloch's Law). As can be seen, a pulse of this duration occurring at pattern offset has no detrimental effect on the strength and there is still no reduction when this period is increased to ½ sec. Equally, delaying the ½ sec. pulse by ½ sec. relative to pattern offset is not accompanied by any significant reduction in strength. The calculated decay slopes are fairly similar, but are a little on the 'shallow' side compared with the values for the equivalent sequence with a totally dark 'OFF' period. It would seem that in order to have an effect the achromatic pulse must have a duration of at least ½ sec. but need not exceed 1 sec.

TABLE 5.4

TEMPORAL SEQUENCE		DECAY SLOPE		STRENGTH	
		VALUES	MEAN	VALUES	MEAN
	10 SEC. ON 1/10 SEC. ACHROM 9 9/10 SEC. OFF	-0.15		2.6	
	10 SEC. ON 5 SEC. ACHROM. 5 SEC. OFF	-0.22		2.4	
	10 SEC. ON 5 SEC. OFF 5 SEC. ACHROM.	-0.22		2.1	

Summary

1. An interpolated period of homogeneous achromatic illumination in the stimulation sequence can impede the process of establishment of the A/E.
2. This period must be longer than ½ sec. but need not exceed 1 sec.
3. The timing of the 1 sec. pulse is critical. The process of establishment of the A/E may be disrupted if the pulse occurs within one second of pattern offset. A reduction in strength may also be observed if the illumination occurs within the second immediately prior to pattern onset.
4. There may be occasions in which an interpolated period of homogeneous achromatic illumination also affects decay slope.
5. The extent of the disruptive influence of a 1 sec. period of illumination depends on the other temporal characteristics of the stimulation sequence. The greatest reduction is observed when both 'ON' and total 'OFF' are 1 sec., and the smallest when the 'ON' is 1 sec. and the total 'OFF' is 10 sec. (the period of illumination occurring at pattern offset). A substantial reduction occurs when the 'ON' period is 10 sec., but the extent is independent of the length of the total 'OFF' period.

CHAPTER 6: DISCUSSION

6.1 Introduction

The findings summarised in Chapters 3 and 4 indicate that strength and decay of the A/E can be influenced by both the total duration of adaptation and the way in which this is fragmented into periods of exposure to coloured patterns and periods of darkness. In this chapter we shall consider how these bear on results recently published by others working in the field of visual information processing, and their implications for the theory of the McCollough Effect.

6.2 The time course of establishment and decay of the McCollough Effect

McCollough (1965) was the first to point out that the A/E may persist for several hours following only a few minutes exposure to the adapting stimuli. With the introduction of quantitative techniques for assessing the strength of the A/E (Riggs et al, 1973; 1974; MacKay & MacKay, 1973(a), (b)) it became possible to confirm these reports and to describe the time course of both establishment and decay.

6.2.1 The time course of establishment

The MacKays did not systematically investigate the time course of establishment, but this question was considered by Riggs et al (1974). They exposed subjects to alternating orthogonally-oriented coloured gratings, each eye pattern being exposed in turn for 5 sec. and the alternation continuing for some time. The effect of the total duration of exposure to this alternation was studied, for durations in the range 15 sec. to 2½ hrs. There were eleven conditions in all, each of six subjects being exposed on separate days to one of these. A/E strength was assessed by means of a colour-cancellation technique. The test card consisted of two achromatic gratings placed side-by-side, the orientations being identical to those of the adapting patterns. The subjective appearance of colour on each half could be neutralised by rotation of a smooth disc which added colour of approximately the complementary wavelength, so that the apparent colours on the whole card could be neutralised. Angular rotation of the disc was calibrated in terms of colimetric purity. The mean of the settings for the two halves was taken as a measure of A/E strength. Testing was repeated at roughly equal logarithmic intervals until full decay of the A/E had occurred. Strong A/E could not be measured initially because of limitations of the testing apparatus, so the subject simply waited until colour matches could be made and then continued as normal.

Estimates of the time course of establishment of the A/E were derived using data values extrapolated from decay plots. The measured strength at 1, 10, 100 and 1000 min. after exposure was plotted against the logarithm of inspection duration. It was concluded that "The increase in aftereffect is a roughly linear one when plotted against a logarithmic scale of inspection time, but there is some evidence of a positive acceleration. A log-log plot gives a more nearly linear display, but shows an obvious negative acceleration for very long durations of inspection" (Riggs et al., 1974, p538-539).

The data presented in Chapter 4 are equally limited for the longer adaptation durations, for the same reasons. The data points are the readings taken at 1 min. after the end of exposure and the plots are therefore similar to one of those presented by Riggs et al (1974). Over the range of strengths that could be measured, it was shown that there was a clear positive acceleration on a linear-log plot, but the process is approximately linear on log-log co-ordinates. Riggs et al (1974) do not show plots of results on log-log co-ordinates, but the data presented here are consistent with their statement that a better fit is obtained on log-log co-ordinates. In addition, the results presented here indicate that the rate of increase in strength is approximately the same for four of the temporal sequences of stimulation (there is uncertainty surrounding the other two sequences because of the variability in strength associated with lengthening of the adaptation duration).

Both sets of results show convincingly that A/E strength increases with longer exposure durations. The time course of this process can be shown for exposures up to about 15 or 20 min., for longer exposures initial A/E strength tends to go outside the range of the measuring apparatus. The plots presumably flatten out at very long exposures, but neither study has provided evidence as to the point at which saturation is reached.

6.2.2 The time course of decay

The time course of decay is a more complicated issue. Systematic differences related to the characteristics of the temporal sequence of stimulation were noted in Chapters 3, 4 and 5, and these will be discussed in a later section. Here we will be concerned with some general features of decay process, and the relation to adaptation duration. MacKay and MacKay (1973 (b)) were quite certain that over most of its time course the decay was best described by a negative power function. The equipment used by MacKay and MacKay for measuring A/E strength was as described in Chapter 2 of this thesis, and is essentially a colour neutralising technique. They found that strength at first decays more rapidly, then more slowly, than a simple exponential function. "In log-log co-ordinates the data for all ten subjects so far tested are well fitted by straight lines with an average slope of about -1/3." (MacKay &

MacKay, 1973 (b), 38P).

Riggs et al (1973; 1974) were not so clear. At first they stated that the "... decay function is nearly linear on log-log coordinates." (1973 p1287). Later, they seemed to modify their position. Most of their data was presented on linear-log co-ordinates, which they thought gave a nearly linear curve (see also White, 1976). However, they went on to state that curves for relatively high degrees of A/E are negatively accelerated "... and would be almost as well described in their middle sections by a double logarithmic fit. Such a fit does not succeed, however, in representing the data at either the high or the low extremes of ordinate values (1974, p538). It is unfortunate that many of the results presented in this paper show relatively few data points for the first ten minutes of decay.

The general problem of whether the data are better fitted by a straight line on log-log or linear-log co-ordinates was considered in Chapter 3. The plots of results show that over most of its course, decay is reasonably linear on log-log co-ordinates (see Appendix E). A statistical analysis of these results indicated that correlation values were high (usually of the order of 0.95) irrespective of whether the log was taken of both time and strength, or of only time. This implies that for the majority of results neither function has clear preference over the other in describing the time course of decay. Moreover, it became clear that a correlation analysis would not provide clear evidence of deviations from linearity on either set of co-ordinates. All the data presented in Chapter 4 were therefore plotted on both sets of co-ordinates, although mainly log-log plots are presented. For the majority of results it was difficult to choose one function in preference to the other as clearly providing a better description of the time course of decay, at least over the restricted time period studied in these experiments. It was not considered to be within the scope of the project to attempt to find a mathematical function which would handle all the data. Moreover, the systematic differences in decay function related to the temporal parameters of the stimulation sequence may indicate that a single function would not be adequate in dealing with all the data.

The statistical analysis of data presented in Chapter 3 revealed one further point of interest in the context of the present discussion. When the log was taken of both strength and time values, the statistically estimated strength for the reading taken at 1 min. after the end of exposure was generally higher than the measured strength, whereas it tended to be lower when the log was taken of only the time values. A similar finding emerged in relation to the last reading. This systematic difference is further evidence that neither function provides a completely adequate description of the time course of decay.

Riggs et al (1974) further suggested that there is a high positive correlation between strength at 1 min. after the end of exposure, and the decay slope calculated from strength and log time values by the method of least squares. That is, calculated decay slope becomes steeper with increase in initial strength. MacKay and MacKay (1973 (b)) estimated the decay slope from data plotted on log-log co-ordinates. They found that the average value of the decay slope for all subjects was about -0.33, and pointed out that weaker A/E yield a lower line of similar slope. The implication was that on log-log co-ordinates decay slope is independent of initial strength, but this problem had not been systematically studied. There would seem to be no real inconsistency between these results. Both imply that the A/E decays more quickly immediately after the end of exposure, and that the stronger the initial effect, the more rapid is this critical rate of decay.

The experimental data and statistical analysis presented in Chapter 3 support this conclusion. The decay slopes calculated from the logarithm of strength and time data showed no systematic change associated with increase in either initial A/E strength or length of adaptation duration. When the logarithm was taken of the time values only, calculated decay slope increased systematically with lengthening of the adaptation duration.

However, the results presented in Chapter 4 would seem to require modification of this basic picture, and add the complicating factor of systematic differences related to the temporal parameters of stimulation. For a number of temporal sequences of stimulation, decay slopes, calculated after taking the logarithm of time and strength, remained reasonably stable over a wide range of initial strengths and adaptation durations. This was the case for the 5 sec. ON/0 sec. OFF sequence, these being the temporal parameters also used by Riggs et al (1974). For three of the sequences, decay following a prolonged period of adaptation was characterised by an unusually steep decay slope, decay being approximately linear on log-log co-ordinates. These steeper decay slopes indicate a quantitative difference from results for shorter exposures for the same sequence, and may be related to some point of "saturation" of the mechanism involved.

The series of results for the ½ sec. ON/5 sec. OFF sequence also show unusually steep decay slopes for both intermediate and prolonged exposure durations. Unlike the case just considered, decay of these A/E was found to be non-linear when plotted on log-log co-ordinates. These results were also plotted on linear-log co-ordinates but the data did not show a better fit to a straight line on this plot (the result for the 50 min. adaptation is a marginal case). A number of other results presented in Chapter 4 were also associated with steep decay slopes and non-linearity of decay on log-log plot, and these were usually associated with temporal sequences having a short 'ON' period and a relatively long 'OFF'. This feature of the results will be considered in a later section of this Chapter.

The results for short and intermediate adaptation durations for the 1 sec. ON/10 sec. OFF sequence are also characterised by steep decay slopes and non-linear decay on log-log plot. However, prolonging the exposure duration was associated with a decrease in the calculated slope of the decay line, and the decay curve became reasonably linear on a log-log plot. It is worth noting that the initial strength associated with the 50 min. adaptation is very similar to that of the previous sequence with the same exposure duration, but the characteristics of decay are different. Similar features characterise the results for the 10 sec. ON/10 sec. OFF sequence, calculated slopes being steeper and decay non-linear on log-log plot for short adaptation durations, but normal slopes and linear log-log plots being associated with intermediate exposure durations.

These features were not evident in results for the other three sequences, even though some exposure durations were shorter than for the sequences just discussed. Indeed, these unusual decay characteristics do not correlate across sequences with either adaptation duration or initial A/E strength. The occurrence of the steep decay slopes and non-linearity of decay on log-log plot may indicate a qualitative difference in the mechanism involved, especially for the sequences with short ON/long OFF periods (see later), but in terms of the other sequences are more cautiously interpreted as suggesting that some internal threshold level is not reached when exposure durations are short. Systematic differences between sequences in build-up of A/E strength may underlie these differing results, and suggest that more extreme exposure conditions would be required under certain circumstances before this threshold level is reached. One would expect decay for all temporal sequences to become non-linear on log-log plot if adaptation duration were made sufficiently short. If this interpretation were correct, it would imply that these decay characteristics are not critical to our general description of the time course of the McCollough Effect.

6.2.3 Summary

In summary, there is clear evidence that A/E strength increases over a wide range of exposure durations. Limitations of the measuring apparatus in both studies generally only permitted the time course of establishment to be followed over periods of 20 min. or so of exposure. Over this duration, the time course is reasonably well described by a straight line on log-log plot. Exceptionally, build up of strength was shown to continue up to 50 min. of exposure. There was no clear evidence that a saturation level had been reached so far as A/E strength was concerned, but unusually steep decay slopes associated with prolonged exposure may be related to this factor. Decay over a prolonged period was shown to be reasonably well fitted by a straight line on log-log co-ordinates. However, the evidence indicated that a log-log plot was not clearly superior to a linear-log plot in describing the time course of decay of the majority of results presented in the parametric study. Neither form of analysis is completely adequate. Systematic differences in the description of the time course of decay may relate to the temporal parameters of the stimulation sequence. Decay slope on log-log plot remains reasonably stable over a range of exposure durations and initial strengths. Changes in decay characteristics at the two extremes of exposure duration may not be significant for our general description of the time course.

6.3 Temporal variables in relation to other forms of visual adaptation

6.3.1 Introduction

Studies of the effect of prolonged exposure to achromatic gratings have utilised measures of the strength of after-effect on suprathreshold test patterns, and changes in the threshold for detection of similarly oriented gratings. These techniques have revealed distortions of size and raised detection thresholds for similarly oriented test patterns. It has been assumed that these aftereffects result from depression of sensitivity of the units affected by the adapting stimuli (Gilinski, 1968; Blakemore & Campbell, 1969 (a),(b)). While not wishing to suggest that the mechanisms underlying contingent and non-contingent A/E are necessarily identical, a number of points concerning the latter group are pertinent to the findings presented in this thesis.

Firstly, recent evidence now indicates that certain non-contingent A/E may also have longer time courses of induction and decay than originally thought. These findings provide important comparisons with the results presented here. These studies also show that initial strength and persistence may vary independently of each other (e.g. lengthening exposures may prolong the persistence of the after-effect without influencing the initial effect). This implies that the two features may be only partially related.

Secondly, in assessing estimates of the time course of establishment and decay, it is important to consider the technique used. There is now evidence from studies of analogues of the McCollough Effect which raise doubts as to the sensitivity of the threshold elevation technique to long-lasting changes induced by prolonged exposure periods.

Finally, it is clear from a review of the literature that researchers have not analysed temporal parameters of stimulation very carefully. In considering the question of the time course of induction and decay of non-contingent A/E, they have therefore failed to distinguish between the effect of the 'ON' period and the effect of the total cycle period. This may in part relate to the fact that usually only one grating orientation has been used in the exposure condition. Despite the absence of systematic studies of the influence of the temporal parameters of the stimulation sequence, some evidence suggests that the mechanism involved has a critical integration time period of a second or two.

For purposes of clarity it will be convenient to consider these findings, before discussing the results presented here concerning the influence of the discrete period of stimulation on strength and decay of the McCollough Effect.

6.3.2 Adaptation to achromatic gratings and the time course of threshold elevation effects.

Threshold elevation techniques were developed by Campbell's group (Campbell et al, 1965; 1966 (a), (b)) as a means of studying human orientation selectivity. Blakemore and Campbell (1969, (a),(b)) generated sinusoidal gratings on an oscilloscope. The contrast of the grating could be varied without alteration of the mean luminance. Contrast thresholds for detection of the test grating were first determined, and subjects were then exposed for a short period to a high contrast grating set 1.5 log units above subjective threshold. Detection thresholds were subsequently found to be elevated, recovery to the pre-adaptation level typically being described by an exponential function with a time-constant of about 20 sec.

The time course of induction of this effect was found to be similarly short. Subjects were adapted for various periods from 5 sec. to 100 sec. and the rise of thresholds was determined immediately after each adaptation period. The rise in the level of the effect reached a plateau after about 1 min. of adaptation. Adapting gratings of higher contrast produced a greater rise but the time course was similar. Similar results were found in relation to the time course of adaptation of the visual evoked potential.

These results indicate that the time course of both induction and decay of the threshold elevation effect is short. However, it has now been shown that these threshold elevation effects may persist for several hours. Heggelund and Hohmann (1976) adapted subjects to a high contrast vertical grating for one hour and found that thresholds were elevated for ½ to 1 hr. when the eyes received normal stimulation in the post-adaptation period. These effects could be made to persist for up to 3 hrs. if the eyes were blindfolded between testing sessions in the post-adaptation session. This is consistent with the findings of MacKay & MacKay (1974; 1975; 1977) that the McCollough Effect is retained in darkness. Only one adaptation duration was used by Heggelund and Hohmann, so there is no further evidence on the course of establishment of this effect, but the report does indicate that a prolonged period of stimulation can give rise to effects which persist over an extended period. This time period is shorter than for the McCollough Effect, but direct comparisons are difficult for two reasons. Firstly, only one grating orientation was used for adaptation and this was continuously visible for inspection by the subject. Secondly, estimates of time course may vary systematically depending on whether test stimuli are presented at threshold or suprathreshold luminance levels.

6.3.3 The time course of the size A/E

Blakemore and Sutton (1969) discovered a new A/E and investigated some of its temporal characteristics. They reported that the perceived size (bar width) of a grating is distorted following inspection of a grating of fixed spatial frequency. Test gratings narrower than the adapting grating appear even narrower and test gratingswider appear even wider. This A/E has a longer time course of induction than the threshold elevation effect reported by Blakemore and Campbell (1969, (a) (b)). The magnitude of the distortion reached a peak after 2 or 3 min. of adaptation. Furthermore, the time course of recovery was longer. For short adaptations of about 60 sec., recovery was found to be complete in about the same time. But with long periods of maintained adaptation (sometimes of more than 40 minutes) a significant A/E could be detected more than 4 hrs. later. Therefore, prolonging the adaptation period beyond 3 min. had no further influence on the initial magnitude of the effect, even though the persistence of the A/E could be prolonged. This latter finding is of some considerable interest. It indicates that some aspects of the changes underlying the A/E are not reflected in the initial estimates of magnitude. This may simply indicate a limitation of the measuring technique, or that the initial effect and persistence are only partially related features. This situation also occurs under some circumstances for the McCollough Effect (see Chapter 4, and later in this Chapter).

6.3.4 Analogues of the McCollough Effect derived from threshold elevation studies

One problem in relation to the A/E considered is whether the differences in time course are related exclusively to the phenomena being studied, or whether they are in part related to the techniques used to assess effect of prolonged exposure to suprathreshold stimuli. Some suggestive pointers emerge from the discovery of analogues of the McCollough Effect derived from threshold elevation studies. Three questions are of importance in relation to these studies. Firstly, are thresholds elevated for detection of a coloured grating following adaptation to a high contrast coloured grating? Secondly, is this threshold elevation effect wavelength-specific? Thirdly, what is the time course of these effects?

May (1972) was the first to demonstrate the threshold elevation effect. One eye of the subject was adapted for 15 sec. to one of three high contrast adapting gratings coloured red or green. Each subject was adapted to each orientation and colour in turn. Immediately after adaptation, the subject had 3 sec. to adjust the luminance of a low contrast vertically oriented grating until the pattern (though not necessarily the colour) was just visible. Contrast thresholds were elevated only when the test grating was the same colour and orientation. Comparing results when the test and adapting fields were the same orientation showed a statistically significant difference related to the colour of the test and adapting condition. Similar effects were found in relation to space frequency adaptation. This result therefore demonstrates that only a very short adaptation period is necessary for wavelength-specific threshold elevation.

The wavelength specificity has been confirmed by Maudarbocus and Ruddock (1974). Lovegrove and Over (1973) have shown colour selectivity in contour masking, and Broerse et al (1975) wavelength specificity in the tilt A/E when the adapting and test patterns were presented to the same eye. By contrast, Sharpe (1974 (a), (b)) and Timney (1976) have argued that this threshold elevation is not wavelength specific, but there are problems with both papers. Timney presented pooled results for a number of subjects, and it is already known that the strength of effects may vary in relation to the colours used (May, 1972) and between subjects. Sharpe's procedure was basically weak in that the technique employed was only designed to isolate colour channels at a peripheral stage (see Green, 1965) and cannot be taken to indicate anything about the nature of the units affected at the cortical level (which could, for example, be broad-band). His finding that thresholds were elevated whether or not test and adapting colours were the same therefore may not provide evidence for inhibitory inputs to cortical cells, though it is still difficult to explain the contradictory results regarding wavelength specificity. The issue is not completely settled, but the balance of evidence is perhaps in favour of wavelength specificity of threshold elevation effects.

The time course of establishment and decay of threshold effects have not been studied in detail so far as the author is aware. However, in one interesting study a comparison was made of the persistence of adaptation and threshold effects (Timney et al, 1974). Subjects adapted monocularly for 90 min. to alternating red and green gratings. Thirty minutes after the end of adaptation, test procedures determined thresholds for both orientations and for red, green and white gratings. At this time there was no evidence for an elevation of thresholds, though control studies had established an elevation of thresholds immediately after the end of adaptation. However, a normal McCollough A/E was clearly present and persisted for 24 hrs. or more.

The results of Timney et al (1974) suggest that here the technique is tapping only a process with a short time constant and is insensitive to processes of recovery which are more prolonged. However, it should be remembered that Heggelund and Hohmann (1976) have shown that thresholds may be elevated for half an hour or more following adaptation to achromatic gratings. This raises two interesting questions. Firstly, is the technique equally insensitive to processes underlying establishment of the McCollough Effect which have a long time course? Secondly, does prolonged adaptation to achromatic gratings involve processes of establishment and recovery with a long time course and which are not adequately revealed by this technique?

6.3.5 Evidence for a critical integration time related to a brief period of exposure to achromatic patterns.

For the non-contingent effects, there have been no completely satisfactory studies of the time course of their establishment or decay. In part because only one grating orientation has been used, no attempts have been made to separate possible influences by the total period of exposure and the exposure sequence. However, a number of reports do provide evidence that some process underlying adaptation to achromatic lines or gratings takes a second or two to reach a steady level.

Gilinski (1968) first determined her subjects' identification thresholds for a test grating following brief exposure to a non-striate adapting flash. At this threshold setting of luminance and duration, probability for correct identification of the orientation (vertical or horizontal) of the target was determined following exposure to one of these at a suprathreshold luminance level. Exposure duration of the adapting grating was varied from ¼ sec. to 8 sec. Fig. 6.1 is taken from Gilinski's 1968 paper. The curve representing correct identification when adapting and test orientations were the same starts

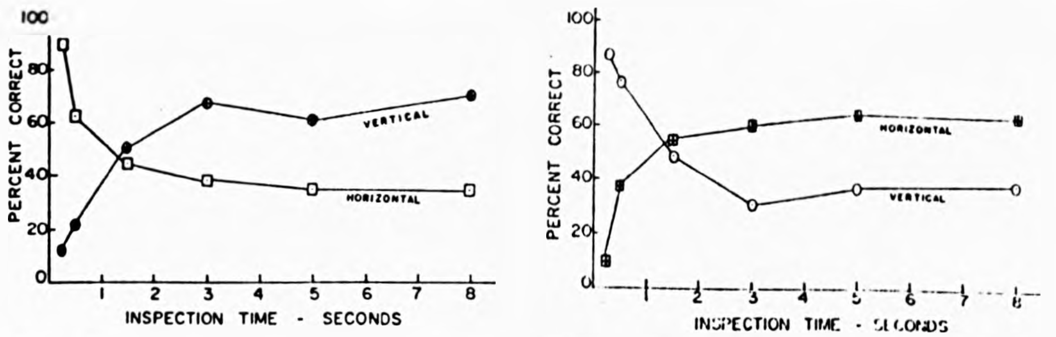


FIG. 1. Relative frequency of detection of the horizontal acuity target following exposures of various durations to horizontal lines (squares) and to vertical lines (ovals). Each point is based on 100 randomized presentations of the horizontal test stimulus; observer, GK.

FIG. 2. Relative frequency of detection of the vertical acuity target following exposures of various durations to horizontal lines (squares) and to vertical lines (ovals). Each point is based on 100 randomized presentations of the vertical test stimulus; observer, GK.

FIG. 6.1 (From Gilinski, 1968)

at a high level and drops below the 50% point for exposure durations between 1 and 2 sec. Conversely, the curve for correct recognition when the test grating was orthogonally oriented to the adapting pattern starts at a low point and climbs as the exposure duration is lengthened, crossing the other curve when exposure durations are between 1 and 2 sec. The separation between the two curves is maintained for longer adaptations. Apart from implying some form of interactive process between visual responses to the two orientations, the results are of particular interest in relation to the time course of the observed effects. Some process initiated by the adapting stimulus takes about 1 to 2 sec. to reach a steady level, and this process is involved in depression of sensitivity to test gratings of similar orientation.

In a second experiment, Gilinski (1968) measured the presentation time necessary for correct recognition of the test grating following various periods of exposure (0.1 sec. to 5 sec.) to a grating of the same or different orientation or to a non-striate pattern. Four orientations were used (horizontal, vertical, left-oblique and right-oblique) and all possible combinations of test and adapting pattern were studied. At the shortest adaptation duration (0.1 sec.) recognition thresholds were about 0.5 sec. for all test and adapting conditions, and remained at about this level as adaptation duration was lengthened for all conditions except that in which test and adapting orientations were the same. In this latter situation, the length of exposure required for correct recognition increased when the adaptation duration exceeded 1 sec. Lengthening adaptation beyond this point was associated with an increase in recognition thresholds, which sometimes exceeded 11 sec. (the maximum possible test exposure). The rate of increase varied systematically with the orientation of the adapting grating.

These results of Gilinski are of interest because a systematic study was made of the effects of temporal variables over a range of a few seconds. They show that some process affecting detection and recognition of a subsequently presented test pattern takes a minimum of a second or two to reach a steady level. A number of other phenomena related to contour processing have been reported to have a growth time constant of about a second or two. While these studies are not directly applicable to the McCollough Effect, they provide further evidence of the possible order of magnitude of temporal events related to contour processing.

Andrews (1965) has shown that the perceived orientation of a line is highly unstable if the period of presentation is less than about ½ sec., and smaller changes can still be observed even when the exposure period is 1 sec. Andrews concluded that some process underlying perception of contours requires about 1 sec. to reach a steady level and thus stabilise judgement of orientation.

Blakemore, Carpenter and Georgeson (1970) and Carpenter and Blakemore (1973) have reported that the angle expansion effect has a short time course of induction. Subjects viewed a visual display containing three lines. Two formed an angle, one line being fixed and the other movable so that the size of the angle could be controlled by the experimenter. The third was located nearby, the orientation of this being under the subject's control. The subject's task was to set the orientation of the single line parallel to the fixed line of the angle. This technique provided a measure of the subjects perception of the size of the angle. The apparent size was found to vary systematically with the size of the angle, acute angles appearing to be expanded and obtuse angles contracted. Subjects typically took 30 sec. or less to make the orientation adjustment, indicating that the time course of establishment of this effect is rather rapid.

Two further experiments were conducted to study more carefully the time course of establishment. In the first, the stimulus display was presented for 2 msec., every 5 sec. instead of being shown continuously. This procedure had no effect on the magnitude of the distortions. In the next experiment, the original procedure was repeated but the subject made each setting as quickly as possible - in 2 to 4 sec. - and then looked away for at least 15 sec. before repeating the procedure. This also had very little influence on the magnitude of the distortion. It was concluded that the process producing this phenomenon has a characteristic growth time constant of less than a second or two.

6.4 Evidence for critical integration time periods underlying the McCollough Effect.

6.4.1 Introduction

It has been pointed out that research into temporal aspects of non-contingent A/E has failed to separate the influence of a total period of adaptation from that of the temporal sequence of presentation of the adapting pattern(s). In a preceding section of this chapter the influence of the total duration of adaptation on strength and decay slope of the McCollough Effect was discussed. The data presented in chapters 4 and 5 indicate that systematic changes in both initial strength and decay slope correlate with manipulation of the temporal parameters of the stimulation sequence. Both the length of the 'ON' and the 'OFF' period may exert a critical influence. Further, differences relate to whether the 'OFF' period is completely dark or illuminated with a period of achromatic light. It will be convenient to consider these results under two broad headings. Firstly, the changes in strength and decay slope which correlate with increase in the length of the 'ON' or 'OFF' periods up to about a second or two and, secondly, the changes which continue with further lengthening of these periods.

6.4.2 Changes in A/E strength and decay slope correlated with variation in the length of the 'ON' or 'OFF' periods over the range ¼ sec. to 2 sec.

6.4.2.1 Changes correlated with the length of the 'ON' period.

In relation to the timing values used, it was thought that 'ON' periods of ¼ sec. were about the shortest that could be used with the apparatus described, as the energy factor intrudes for shorter exposure periods in the case of coloured stimuli presented at threshold. Regan

(1971) has shown that there is an analogue of Bloch's Law operative in the colour domain, the temporal integration period being longer than for achromatic light pulses. For pulses adjusted to subjective threshold, these critical periods are approximately 110 msec. for long wavelengths and 250 msec. for medium and short wavelengths. Although stimuli in the present experiments were well above threshold luminance, Brindley (1970) and Haber and Herschenson (1973) report that Bloch's Law has been verified for achromatic pulses above threshold. The possibility remains that the energy factor could confound interpretation of any changes observed in the A/E strength for chromatic light pulses with a duration less than 250 msec. In addition, the "rise time" for the fluorescent tubes (i.e. the time taken for tube luminance to reach 90% of peak strength) of the tachistoscope was approximately 20-25 msec., which could also become an important factor when the 'ON' period is very short.

The results of five series of experiments presented in Chapter 4 provide strong evidence that changes in the length of the 'ON' period over the range ¼-1 sec. have critical influence on A/E strength. In all cases, lengthening the 'ON' for a fixed duration of adaptation is associated with an increase in initial A/E strength. For each series, the rate of increase in strength is steepest over this range of 'ON' periods, increase in A/E strength being approximately linearly related to 'ON' period. Since this feature is observed whatever the length of the 'OFF' period, the key factor must be the 'ON' period itself. The most persuasive series showing these changes in strength is that in which the 'OFF' period is 0 sec., when the subject is exposed to coloured pattern stimulation for the whole of the adaptation duration. These findings imply that the mechanism underlying the A/E integrates the visual input over a period of at least 1 sec.

There are no observable systematic changes in calculated decay slope correlated with the length of the 'ON' period over this range of 'ON' periods.

6.4.2.2 Changes correlated with the length of the 'OFF' period

It is clear from these results that the 'ON' period is not the only critical temporal parameter. Over the range of 'ON' period under consideration, reduction in the length of the 'OFF' period from 10 sec. to 1 sec. is associated on each occasion with a steepening of the rate of increase of A/E strength. One possible interpretation is that the proportion of 'ON' to 'OFF' is critical. However, a systematic study of the influence of the 'OFF' period for a range of 'ON' periods from ¼ sec. to 10 sec. provides strong evidence that this is not itself a satisfactory explanation. If the proportion of 'ON' to 'OFF' were the only factor, one might expect that the changes in strength associated with lengthening the 'OFF' period from 0 to 10 sec. would be described by a monotonic function. This is not the case. The results for one subject show that there is an increase in both strength and decay slope associated with lengthening of the 'OFF' period from 0 to 1 sec. (there is one exception to this rule, which will be considered later). More limited data suggests that there is a sharp reversal of this trend associated with further lengthening of the 'OFF' period to 2 sec. Thereafter, changes in strength and decay slope do not vary systematically with the length of the 'OFF' period; the 'ON' to 'OFF' ratio may become an important factor.

A restricted number of experiments on two other subjects, using a 5 sec. 'ON' period, show that a similar sequence of changes in strength are associated with lengthening of the 'OFF' period. However, both differ from the previous results in showing peak strength being reached when the 'OFF' period is 2 sec., a sharp decrease occurring with further lengthening of the 'OFF' to 3 sec.*

*see next page

These results suggest that a qualitatively distinct process is operative during the first second or two of darkness following offset of the coloured pattern stimuli, and that the nature and duration of this process is independent of the length of the preceding period of stimulation. The processes occurring during this time period affect both initial strength and decay slope. This interstimulus time period is clearly optimal with respect to initial strength. The unusually steep calculated decay slopes reflect changes in the initial rate of decay (i.e. over the first 10 min. or so), rather than shortening of the total persistence of the A/E.

Interpretation of these results is difficult, but it may be that two factors are important. In the first place, some process may be operative during this 1 or 2 sec. period which has the effect of "boosting" the changes initiated by the preceding period of coloured pattern stimulation. When the 'OFF' period is shorter, this processing is curtailed, or interrupted, by further coloured pattern stimulation.

The second factor may be the way in which the visual system integrates successive stimuli. One possibility is that when the coloured pattern stimuli occur sufficiently close in time, the neural consequences of the first may "overlap" those of the second. That is, the second stimulus may serve to maintain the neural activity initiated by the first, so that

---

*Footnote

There is limited evidence from one subject only regarding changes in decay slope associated with lengthening of the 'OFF' period. These results indicate that the peak in decay slope is associated with a 1 sec. 'OFF' period, a sharp decrease in calculated slope occurring with further increase in the 'OFF' to 2 sec. If this finding proved replicable, it would suggest that the sharp point of reversal related to the sequence of changes in decay slope need not be the same as that for A/E strength.

there is a process of temporal integration. When the 'OFF' is shorter than this critical period the temporal overlap interrupts the important processing operations continuing after offset of the first stimulus. When the 'OFF' exceeds this critical period, even if by only a second or so, the activity related to the processing of the first stimulus may have diminished sufficiently to make it effectively isolated from the processing of the successive stimulus. With relatively long 'OFF' periods, the proportion of 'ON' to 'OFF' may become important and this will be considered later.

The evidence would suggest that the neural activity related to a period of coloured-pattern stimulation persists for only a second (or two seconds for some subjects) after offset of the pattern, and that this time course also defines the optimum period for separation of successive stimuli. In this way it is possible to account for the observed changes in strength of A/E.

The changes in decay slope with lengthening of the 'OFF' period may be causally related to the changes in initial strength. The graphs presented in Appendix G indicate, in so far as one can tell from the restricted decay period studied, that the time to A/E threshold is not affected. Rather, the changes in decay slope reflect the increased rate of decay over the first ten minutes or so after adaptation. The steeper calculated slopes associated with 1 sec. 'OFF' periods therefore reflect a "straightening-out" of the curve over the initial phase of decay, rather than a change in the slope of the line as a whole.

6.4.2.3 Further evidence on the role of the interstimulus period.

Further evidence that a qualitatively distinct process is operative during the first second after coloured pattern stimulation is provided by the results of experiments in which a period of achromatic illumination was introduced into the stimulation sequence. These results show that establishment of the A/E can be impeded by the inclusion of a period of achromatic illumination in the adapting sequence. Two basic findings are relevant to the results just discussed. Firstly, in order to exert an impeding effect the period of achromatic illumination must be longer than ½ sec. but need not exceed 1 sec. Prolonging the period beyond 1 sec. is not associated with any increase in the magnitude of the impeding effect.

Secondly, the timing of the achromatic relative to coloured-pattern illumination is critical. The impeding influence of a 1 sec. period of achromatic illumination is observed only if it occurs immediately after offset of coloured pattern stimulation, or immediately prior to its onset. The importance of these periods was confirmed by varying the temporal location of the achromatic pulse within a fixed 'OFF' period. Strength was reduced relative to equivalent temporal sequences with a totally dark 'OFF' period only when the pulse occurred in one or other of these critical time periods. The impeding effect of an achromatic pulse in the first second after pattern offset was verified for two other temporal sequences with shorter 'ON' periods, but the importance of the 1 sec. prior to pattern stimulation was not confirmed for any other sequence. The limited results also raise the possibility that the precise nature of the disruptive effect of an achromatic pulse may vary depending on whether it occurs prior or subsequent to coloured pattern stimulation.

Interpretation of these findings is aided by reference to theories developed from studies of visual masking. A central idea arising from this work is that the neural consequences of visual stimulation may outlast termination of the stimulus itself (Neisser, 1968). Consequently, the detection, recognition or phenomenal appearance of a target stimulus can be affected by prior or subsequent presentation of a diffuse or patterned masking field, provided that the target and mask occur in close temporal and spatial proximity and certain other criteria are met.

There is no single explanation for all the reported effects, but three basic ideas have emerged (Kahnemann, 1968; Haber and Herschenson, 1973; Dick, 1974). The first is that some observed effects may simply relate to the summation of energy of successive stimuli. In this context, it is worth noting that the masking effects of a pulse of unpatterned light do not show up under dichoptic conditions, which suggests that the effect may be retinal. Secondly, a closely related theory suggests that there may be a process of neural integration related to more complex features of the two stimuli. Finally, and particularly relevant to the backward masking situation, is the idea that processing of the target may be 'stopped', or disrupted by the subsequent masking stimulus.

How, then, may we account for the impeding influence on establishment of the McCollough Effect of a pulse of achromatic light at pattern offset? If we assume that the processing of the coloured-patterns continues for a short time after offset of the stimulus, one possible explanation is that the achromatic pulse somehow disrupts, or interferes with, this processing. This interpretation is appealing because of two experimental findings reported here. The first is that a 1 sec. dark 'OFF' period appears to be optimum for establishment of the A/E. Secondly, in order to exert an impeding influence on establishment, a pulse of achromatic light must occur in the 1 sec. immediately after pattern offset, and must have a duration of between ½ and 1 sec. The correspondence between these time periods suggests that the neural processing of the McCollough patterns continues for up to a second after stimulus offset, and this processing may be disrupted by other forms of stimulation extending over this critical time period.

Alternatively, the impeding influence may be related to summation of energy of the two stimuli. However, while this factor may partially account for the impeding effect, this form of explanation would seem to be more appropriate in accounting for the findings when the achromatic pulse occurs just prior to pattern onset.

6.4.2.4 Relevance to these results of other reported findings

Hajos (1968) reported that lengthening the interstimulus period from 0 sec. to 2 sec. was associated with increase in A/E strength, for both 1 sec. and 2 sec. stimulus presentation periods. This is consistent with the present findings that with a 5 sec. 'ON' period, initial strength increases with lengthening of the 'OFF' up to 2 sec. (for one subject peak strength was associated with a 1 sec. 'OFF' period). The relevant experiments were not performed for the 1 sec. 'ON' period in that a 2 sec. 'OFF' period was not used. It would be important to confirm that strength continues to rise when the 'OFF' is further lengthened to 2 sec. Alternatively, would the 'ON' to 'OFF' ratio become a critical factor, causing A/E strength to decrease when the 'OFF' becomes longer than the 'ON'?

White (1975; 1976), varying the presentation period of the coloured patterns, with a 0 sec. interstimulus period, reported that optimum presentation rates were, "... on the order of a few seconds per alternation; higher or lower rates yield somewhat smaller scores for A/E strength." (1975, p1200). The rate of pattern alternation was varied over the range from one alternation per inspection period (7.5 min/pattern) to more than sixteen thousand alternations per inspection period (27 msec./

pattern). The fastest presentation rate used here, with a 0 sec. 'OFF' period, was 2 cycles per second (250 msec./pattern), and initial strength was clearly lower than that associated with a ½ cycle per second temporal sequence. In this respect, the results are consistent with the findings of White (1975; 1976). However, the present results show that there is a much sharper decrease in strength when presentation is reduced below the optimum, and that there is very little change with presentation periods up to 10 sec. or so.

6.4.3 Changes in A/E strength and decay slope correlated with lengthening of the 'ON' or 'OFF' period, when these are longer than 1 sec.

The results presented in Chapter 4 show that systematic changes in strength and decay slope occur with changes in both 'ON' and 'OFF' over a wider range of periods and we may now consider their significance. The changes in initial A/E strength are perhaps the easiest to deal with and may be considered first.

6.4.3.1 Changes in A/E strength

Fig. 4.24 suggests that there is an approximately linear relationship between strength and 'ON' period, from 1 sec. 'ON' up to the point at which the 'ON' and 'OFF' periods are equal. This situation cannot be seen convincingly in the results of any one series of experiments but is implied by those of a number of series shown in Table 4.16. We may consider first the experiments in which the 'ON' period was varied for a fixed 'OFF' period. There is an approximately linear rise in strength correlated with increase in the length of the 'ON' period from 1 sec. to 10 sec. for the series with a 10 sec. 'OFF' period. When the 'OFF' period is 5 sec. there is a slight negative acceleration as the 'ON' is increased from 1 sec. to 5 sec., after which there is no change. For the series with ½ and 1 sec. 'OFF' periods, the 'ON' period is equal to or longer than the 'OFF' over the range of interest, and there is no systematic rise in strength associated with lengthening the 'ON' period.

Re-phrasing this interpretation, one could say that the system underlying establishment of the A/E can tolerate up to a 50% reduction in total coloured pattern stimulation without producing any adverse effect on A/E strength, provided that the total adaptation duration remains constant. This can be seen clearly if we next consider several series of experiments in which the length of the 'OFF' period was the independent variable, for several fixed 'ON' periods (see Table 4.16). With a 10 sec. 'ON' period, there is no substantial reduction in initial strength as the 'OFF' period is lengthened to 10 sec. Lengthening the 'OFF' to 100 sec. is associated with an initial A/E strength which is about the same as that for two other temporal sequences having the same 'ON' to 'OFF' ratio (i.e. sequences 1 sec. ON/10 sec. OFF and 20 sec. ON/200 sec. OFF). For the series with a 5 sec. 'ON' period, there is no systematic reduction in strength as the 'OFF' is progressively lengthened up to 5 sec., at which point the 'ON' and 'OFF' are of equal length. Lengthening the 'OFF' period to 10 sec. is associated with a reduction in strength. The absolute length of the 'OFF' period is clearly not the critical factor. Initial strength is identical for both 5 sec. and 10 sec. 'ON' periods when the 'OFF' is 5 sec., but in the latter case lengthening the 'OFF' does not affect strength whereas for the 5 sec. 'ON' period lengthening the 'OFF' to 10 sec. is associated with a reduction in strength. Equally, systematic reduction in initial strength with 'OFF' period is observed for the series with a 1 sec. 'ON' period only when the 'OFF' is longer than 1 sec.; when the 'ON' period is ½ sec. the averaged results are identical for 0 sec. and ½ sec. 'OFF' periods, after which there is a systematic reduction in strength as the 'OFF' is lengthened.

These conclusions are based primarily on the results of one subject. A restricted number of experiments were carried out on a few other subjects for two of the series discussed. For the 10 sec. 'ON' series, the results for one other subject suggest that there is no systematic reduction in strength with lengthening of the 'OFF' period from 1 sec. to 10 sec., while the results for two other subjects over the same range are indicative of smaller A/E being associated with longer 'OFF' periods. For all three subjects, the strength associated with the 10 sec. ON/100 sec. OFF sequence is about the same as that associated with the 1 sec. ON/10 sec. OFF sequence, thus providing support for the idea that the proportion of coloured pattern stimulation does have an effect at more extreme 'ON' to 'OFF' ratios. For the sequence with a 5 sec. 'ON' period, the results of one subject corroborate the picture already described.

The picture is by no means clear-cut, but the results do suggest that the system underlying establishment of the A/E is highly sensitive to the proportion of the total adaptation duration occupied by coloured-pattern stimulation. Whatever the length of the 'ON' period, no systematic reduction in strength is observed as the 'OFF' period is lengthened from 0 sec. up to the point at which the 'ON' and 'OFF' periods are equal, or when total exposure has been reduced by 50%. Beyond this point, A/E strength is approximately linearly related to ON/OFF ratio. Decay slope is in the main unaffected by these parameters of stimulation. (but see next section). No explanation of this feature is obvious.

6.4.3.2 Changes in slope of the decay line

Two series of experiments in which the 'ON' period was the independent variable show systematic changes in the calculated decay slope associated with lengthening of the 'ON' period. Both series had relatively long 'OFF' periods of 5 sec. and 10 sec. The results of one subject for the series with a 10 sec. 'OFF' period reveal that for the shortest 'ON' period a decay slope could not be calculated because of too few data points, but for the 1, 2 and 3 sec. 'ON' sequences calculated slopes were unusually steep. The steepest mean value was for the sequence with a 1 sec. 'ON' period, but the scatter plot of values shows overlap with those for the two longer 'ON' periods, suggesting that there is no systematic change over this range. Moreover, decay is non-linear on log-log co-ordinates for all three temporal sequences, though there is a systematic change in the shape of the plot associated with lengthening of the 'ON' period. Decay for all three sequences is approximately linear on <u>linear-log</u> co-ordinates. Lengthening the 'ON' to 4 sec. is associated with a distinct decrease in the calculated decay slope, and decay is linear on <u>log-log</u> co-ordinates. Further lengthening of the 'ON' period does not seem to be associated with any systematic change in decay slope.

There are only limited results available on three other subjects for this series, and all show the steepest decay slopes when the 'ON' period is 1 sec. For two of the subjects decay is clearly non-linear on log-log co-ordinates. Thereafter, the trends are not clear-cut. The results of one subject show no clear systematic changes associated with lengthening the 'ON' period. Those for a second subject show a clear drop in calculated decay slope as the 'ON' period is lengthened from 1 to 2 sec., after which there is no systematic change. The results for the final subject are indicative of a decrease in decay slope somewhere between 3 and 5 sec. 'ON', but it is not possible to say whether the changes are progressive or defined by a sharp point of transition.

The results for one subject for the series with a 5 sec. 'OFF' period provide some support for the trend described. Again, for this subject a decay slope could not be calculated for the sequence with a ½ sec. 'ON' period, but decay slope is unusually steep for those with 1 and 2 sec. 'ON' periods and there is a distinct "drooping" of the later data points on log-log co-ordinates. Unfortunately, time had not permitted this series to be completed, so that no results are available for sequences with 3 and 4 sec. 'ON' periods. However, the results for the 5 and 10 sec. 'ON' periods are similar and both are distinctly shallower than those associated with the shorter 'ON' periods. This suggests that the characteristics of the decay slope change when the 'ON' period is lengthened to 3 or 4 sec. This result would be roughly in line with that for the same subject on the previously discussed series.

The series of experiments with an 'ON' period of 1 sec. also show systematic changes in decay slope with lengthening of the 'OFF' from 0 to 10 sec. Calculated decay slope becomes progressively steeper and the shape of the plot changes for the two longest 'OFF' periods, becoming non-linear on log-log co-ordinates for the 1 sec. 'ON'/10 sec. 'OFF' sequence. These changes are not seen in the results of similar series having 5 or 10 sec. 'ON' periods.

Do these observed changes in the calculated decay slope and characteristics of the decay plot have any significance for the theory of the McCollough Effect? Ones immediate reaction is to ask whether these unusually steep decay slopes are simply a consequence of the weak A/E usually associated with these temporal sequences of stimulation. If they are, the changes may simply indicate that some internal threshold level has not been reached, in which case these decay slopes may not be critical for our general description of the time course of the A/E or our understanding of the mechanism involved.

There are four factors which, taken together, tend to suggest that the observed changes are not related to the initial strength of the A/E. The most important is that other temporal sequences giving similar initial strengths to those under discussion are not associated with abnormally steep decay slopes or with any significant non-linearity on a log-log plot. Secondly, changes in strength over a wide range do not correlate with changes (if any) in decay slope. Thirdly, there is the limited evidence that some of these results with an abnormally steep decay slope may be better fitted by a straight line on linear-log plot. This suggests that the mechanism underlying the A/E is operating differently under these conditions. Finally, there is evidence that for one subject there is a sharply defined point of change in calculated decay slope though there is no corresponding point of change in critical A/E strength.

These systematic changes in calculated decay slope may therefore be significant for our understanding of the fine time structure of the A/E. The changes for two series of experiments correlate with manipulation of the length of the 'ON' period, and suggest that certain neural modifications may have a time course of as long as 3 or 4 sec. for one subject, though there may be systematic differences between subjects with regard to this critical time period.

The time course of the neural events underlying the observed changes in decay slope are not identical with those related to changes in initial strength. The interpretation of these differences may hinge around a distinction between consideration of the changes induced by coloured pattern stimulation and the effectiveness, or relative permanence, of the induced changes. Coloured pattern stimulation may induce certain neural changes, which are reflected in the measurements of the initial strength of the A/E and are most rapid in the first second or so of stimulation. However, when stimulation is so brief, the induced changes are relatively unstable and the system is more easily capable of restoring itself to a state of equilibrium. However, a slightly more prolonged period of stimulation is capable of "consolidating" these neural changes, which may not significantly affect initial strength of A/E but does prolong the process of recovery.

One can therefore account for the shallow decay slopes associated with long 'ON' and 'OFF' periods (10 sec. 'ON'/100 sec. 'OFF' and 20 sec. 'ON'/ 200 sec. 'OFF'), but relatively weak A/E. Under these conditions the 'ON' period may be substantially longer than the critical time necessary for effective "consolidation". However, if this general line of interpretation is correct, the question is why these unusually steep decay slopes are not observed for all temporal sequences incorporating a short 'ON' period. The results presented here indicate that these 'ON' periods are not generally associated with abnormally steep decay slopes or non-linearity of decay on log-log plot when the associated 'OFF' period is short (1 sec. or less).

The explanation of these paradoxical differences, related to the length of the 'OFF' period, is again based on the idea that processing of the coloured pattern stimuli continues in the first second or so after stimulus offset. This processing may facilitate integration of successive stimuli when these are not separated by more than about one second of darkness. These integrative processes may be capable of making more effective the changes induced by the discrete period of stimulation, when the 'ON' period itself is shorter than the critical time required by the mechanism involved. Maximum "consolidation" may therefore be achieved if either the discrete 'ON' period is equal to or longer than some critical time, or if stimulation is effectively continuous (so far as the mechanism involved is concerned), because of the integration of successive stimuli. This explanation may account for the shallow decay slopes associated with the series of experiments having a 0 sec. 'OFF' period.

6.4.3.3 The differential effect of an interpolated period of diffuse illumination in the stimulation sequence

A further limited series of experiments incorporating a short period of achromatic illumination in the stimulation sequence provide important support for this interpretation of the failure to find abnormally steep decay slopes when the 'ON' and dark 'OFF' periods are short. These experiments consider two important questions. Firstly, the effect of a 1 sec. pulse of achromatic illumination in relation to a limited number of temporal sequences of stimulation. In this respect the important comparison is between the results associated with this stimulation sequence relative to those for the equivalent sequence in which the 'OFF' period is completely dark. Secondly, the differential effect of the interpolated 1 sec. pulse. Here the important comparison is between sequences which include 1 sec. of illumination in the period immediately after pattern offset. These experiments may be considered first in relation to the length of the 'ON' period of the temporal sequence, and then to the 'OFF' period.

For 'ON' periods of 10 sec., insertion of a period of achromatic illumination into the stimulation sequence is associated with a reduction in the strength of the A/E compared with results when this period of illumination is not included. The disruptive influence is independent of the total length of the interstimulus period, the proportional reduction in strength being about the same for the sequences with a 1 and a 10 sec. 'OFF' period. Decay is similar for the two sequences.

However, when the 'ON' period is only 1 sec. the total length of the interstimulus period is of considerable importance in determining the extent of the disruptive influence of the achromatic illumination. When the total 'OFF' period is 10 sec., A/E strength is only slightly reduced (in both real and proportional terms) compared with sequences having a totally dark 'OFF' period, and there is no differential effect on decay slope. Conversely, when the 'OFF' period is 1 sec. and completely illuminated, A/E strength is considerably reduced in both real and proportional terms. Moreover, the period of illumination in this latter sequence gives rise to an abnormally steep decay slope and a non-linearity of decay on log-log co-ordinates. In fact, the result for the 1 sec. 'ON'/1 sec. 'Achrom'. sequence are very similar in terms of strength and decay slopes to those of the 1 sec. 'ON'/10 sec. 'OFF' and 1 sec. 'ON'/1 sec. 'Achrom'/ 9 sec. 'OFF' sequences. One can say that the 1 sec. achromatic interstimulus period has a similar effect to 10 sec. of darkness when the associated 'ON' period is 1 sec. (the results are not identical, in that decay for the sequences with a period of achromatic illumination are not so well fitted by a straight line on linear-log co-ordinates).

A temporal sequence with an 'ON' period of intermediate duration (5 sec.) and 10 sec. 'OFF' period was also used. The inclusion of a 1 sec. pulse of achromatic illumination has a similar disruptive effect to when the 'ON' period is 1 sec.

It has been hypothesised that one effect of a 1 sec. pulse of achromatic illumination at stimulus offset may be to disrupt processing of the coloured pattern just presented, and may prevent integration of successive stimuli when the total interstimulus period is short. Consequently, it may be possible to gain a better impression of the role of the 'ON' period itself under these conditions. On this basis it is possible to account for the observed differences related to the 'ON' and 'OFF' parameters of stimulation.

One would expect a greater disruptive effect if the 'ON' period is less than some critical processing time. This may be the reason for the difference between results for sequences with 1 sec. and 10 sec. 'ON' period, when the 'OFF' period is 1 sec. and completely illuminated. When the 'ON' period is 10 sec. the characteristics of decay are not affected by the achromatic illumination but strength is reduced, this effect indicating some disruption of processing. However, when the 'ON' period is only 1 sec. an equivalent period of illumination affects the characteristics of decay and has a greater influence on strength. This suggests that as far as decay is concerned, this discrete period of stimulation is less than the minimum required for effective "consolidation" of the changes induced by the period of stimulation. It also suggests that a 1 sec. period of stimulation is less effective than a 10 sec. period in terms of build-up of A/E strength, which may also suggest that the mechanism involved has an integration time period of longer than a second.

Why, then, does the pulse of illumination have very little impeding effect when the 'ON' period is short but the total 'OFF' is 10 sec.? It has already been pointed out that a 1 sec. illuminated 'OFF' period associated with a 1 sec. 'ON' period gives rise to results which are in all ways similar to those associated with a 1 sec. 'ON'/10 sec. 'OFF' sequence, but are dissimilar to those associated with a 1 sec. 'ON'/1 sec. 'OFF' sequence. It is therefore proposed that a long dark 'OFF' or a 1 sec. illuminated interstimulus period each have the same effect and that there is no additional impeding influence arising from their combination. In the case of the short 'OFF' period, the pulse of illumination may disrupt ongoing visual processing and prevent the neural consequences of one period of stimulation from overlapping the activity associated with the following stimulus. The long period of darkness also effectively isolates (neurally) successive periods of stimulation. Since there is no active disruption of processing, it must be assumed that the factor of isolation may effectively wipe-out the benefits which accrue from the processing assumed to take place in the first second of darkness after pattern offset.

If this line of argument is correct, the changes in initial strength and decay slope associated with the series with a 10 sec. dark 'OFF' period are indicative of the time course of various stages of the neural modifications which underlies the A/E. Similar results should be observed with similar lengthening of the 'ON' period whatever the length of the 'OFF' period; but provided that it is not less than about 1 sec. and that the first second after pattern offset is illuminated. A minimum 'OFF' period of 1 sec. is stressed because it was shown that an achromatic pulse must have a duration of ½-1 sec. in order to impede A/E establishment.

6.5 Conclusions

McCollough hypothesised that the physiological basis of the A/E is a fatiguing of single units in the visual cortex. Very little work has been done at the single unit level to determine how responses of sensory neurones are affected by prolonged stimulation. Moreover, the studies available (e.g. Barlow and Hill, 1969; Vautin and Berkley, 1977) are not critical to the findings presented here because units were stimulated for only a relatively short period (1 min. in the papers cited), and temporal parameters were not manipulated in such a way as to provide analogues of the psychophysical procedures described here. There is therefore insufficient physiological data available to either support or rule-out McCollough's hypothesis.

Equally, the experiments described here do not constitute a critical test of this hypothesis. However, while not attempting to rule-out the 'fatigue' theory, it is thought that the picture is made more complicated by a number of the findings presented in this thesis. These findings, and the conclusions to be drawn from them regarding the time structure of the McCollough Effect, may now be summarised:-

(1) The mechanism involved is capable of modification by continuous stimulation over a prolonged time. Recovery to its equilibrium state is even more protracted. These conclusions are based on two findings. Firstly, initial A/E strength increases with lengthening of exposure up to one hour or more, without any clear evidence that the point of saturation has been reached. Secondly, decay of the A/E may take up to several days to extinction.

(2) Initial strength of A/E is most critically influenced by 'ON' periods up to about a second or two, longer 'ON' periods having relatively less effect. These facts were interpreted as evidence that the mechanism underlying A/E strength has a critical time constant of

about a second or two.

(3) A further undisturbed second or two may be required for effective 'consolidation' of the induced neural changes. Important evidence supporting this idea are the results showing the effect of an interpolated period of achromatic illumination, and the finding that calculated decay slopes change systematically with the length of the 'ON' period up to about 3 or 4 sec., when the associated dark 'OFF' period is 5 or 10 sec. Moreover, for these short 'ON' periods decay tends to be linear on <u>linear-log</u> co-ordinates. There may be a point of sharp transition between 3 and 4 sec. 'ON', when log-log decay slope suddenly becomes less steep and decay becomes nearly linear on <u>log-log</u> plot. This suggests that the mechanism involved may be operating differently over this range of 'ON' periods.

(4) The lack of correspondence in estimates of the time course of changes underlying strength and decay slope, coupled with the possibility that the mechanism involved may operate differently depending on the length of the 'ON' period, would seem to require (at least) elaboration of an explanation in terms of a single stage mechanism.

(5) The length of the dark 'OFF' period is important, 1 or 2 sec. being optimum in terms of A/E strength. This indicates facilitatory interaction between successive stimuli, even when these are different in terms of colour and grating orientation and are therefore assumed to be exciting different classes of unit.

(6) Further systematic changes in strength correlate with variation of 'ON' and 'OFF' over a wider range of exposure periods. These changes indicate that the mechanism involved is sensitive to the proportion of 'ON' to 'OFF', in addition to the length of each of these alone. In other words, A/E strength is not related simply to the total

duration of excitation of the units assumed to be involved.

(7) McCollough's hypothesis implies that the units involved can be excited only by patterns with specific orientation and wavelength. Nevertheless, it has been shown that other stimuli impede establishment of the A/E, provided that they are presented for a sufficient period immediately before or after exposure to the coloured gratings. There are two groups of findings:-

(a) A pulse of achromatic illumination at pattern offset must have a duration of between ½ and 1 sec. in order to influence establishment of the A/E. This effect was interpreted in terms of disruption of ongoing activity in the second immediately after pattern offset. That is, it was necessary to assume that the mechanism involved was still 'active' even after termination of the stimulus which supposedly excites it.

(b) Achromatic gratings or diffuse colours have a more substantial effect on establishment of the A/E (see Murch, 1976; and Appendix A). Exposure to achromatic gratings or diffuse colour immediately before or after coloured-pattern stimulation is associated with a substantial reduction, or even a wiping out, of the A/E to which the McCollough patterns may be assumed to give rise. The critical time periods are longer than for a pulse of achromatic illumination, typically being of the order of 2 to 3 sec. Therefore, the activity of units assumed to be excited by the coloured patterns may be influenced by stimuli which should not excite them. Theory will have to explain these interactions, and the way in which they may wipe-out the effects of excitation of the units assumed to be involved.

A number of other recently published findings are also thought to complicate the picture, and these are reviewed in Appendix E.

CHAPTER 7

FURTHER EXPERIMENTS SUGGESTED BY THE PRESENT STUDY OF THE ROLE OF THE TEMPORAL PARAMETERS OF STIMULATION

The research reported here was carried out over a 2¼ yr. period. Pressure of time resulted in a number of experimental series being left at an incomplete stage, and other areas remaining untackled. The purpose of this chapter is to indicate the points still requiring clarification, and the way in which the project could be developed experimentally, to deal with various questions raised by the findings presented here.

1. It would be of interest to explore the effects of very long and very short adaptation durations. For long adaptations, the equipment would need to be re-calibrated for matching stronger A/E's. One would then like to follow build-up of A/E strength to saturation level, and to compare the rate of build up for different temporal sequences of stimulation. One would also like confirmation of the observed changes in the slope of the decay line when adaptation is long and initial strength of A/E is high.

For the weak A/E's associated with short adaptations, it would be interesting to confirm the finding that decay becomes non-linear on a log-log plot. It has been suggested (Chapter 6) that this feature may characterise the results of all temporal sequences of stimulation, but that the point at which decay becomes non-linear may vary systematically with the temporal characteristics of the stimulation sequence. These changes associated with short adaptation durations may indicate incomplete "consolidation" of the neural modifications induced by coloured-pattern stimulation; the differences between conditions may reflect the relative efficiency of the various temporal sequences, in "consolidating" the induced neural modifications.

2. The findings presented here indicate that the 'ON' period may have a critical influence on build-up of strength and "consolidation" of the induced neural changes. For this reason, the whole range of 'ON' periods up to about 5 sec. needs a more thorough analysis. The work could be developed by varying the 'ON' and 'OFF' periods systematically, in the way already described in Chapter 4.

(a) Varying the 'ON' period. A number of questions are of interest: (i) Will decay slope, calculated using log.values for time and strength, vary systematically with lengthening of the 'ON' period, particularly for 'OFF' periods between 1 and 5 sec.? In particular, will the same point of transition be observed in calculated slopes, as the 'ON' is increased over the range 2 to 4 sec.? (ii) Since these changes are not observed for the series of experiments with a 1 sec. 'OFF' period, will there be a point of sharp transition between series with different 'OFF' periods, when these changes will cease to be observed; or will there be a progressive change, the point of transition determined by the 'ON' period becoming less distinct on each occasion?

(b) Varying the 'OFF' period. There are two broad questions of interest. (i) For the 'ON' periods of interest (i.e. up to 5 sec.), will decay slope become steeper and decay non-linear on log-log plot with long 'OFF' periods? (ii) Will lengthening the 'OFF' period up to 1 or 2 sec. always be associated with a systematic increase in A/E strength (which may be related to integration processes); or will this only be the case when the 'ON' period is longer than 1 sec.? The situation may be different when the 'ON' period is $\leq$ 1 sec. because the factor of the ON:OFF ratio intrudes over the critical range. It has been suggested that once the 'OFF' becomes longer than the 'ON', A/E strength decreases systematically with lengthening of the 'OFF' period.

3. *It has been suggested (Chapter 6) that* a 1 sec. pulse of achromatic illumination at pattern offset has a similar effect to a long dark 'OFF' period in 'isolating' successive stimuli. A critical test of the importance of the 'ON' period would be to consider the effect of varying this over the range ¼ to 10 sec. In all cases the interstimulus interval would be a 1 sec. period of achromatic illumination. There are two specific questions in mind. (i) Would there be systematic changes in decay slope, as were observed for the series with a 10 sec. 'OFF' period, especially with respect to the point of sharp transition in calculated slope correlated with lengthening the 'ON' from 3 to 4 sec.? Moreover, would there be systematic differences between temporal sequences in the function providing the best description of the time course of decay? (ii) Would there be a similar series of changes in initial A/E strength, with a rapid build up with lengthening of the 'ON' period to 1 sec., followed by a more gradual rise? For the systematic changes associated with lengthening of the 'ON' period beyond 1 sec., would the increase in strength continue up to 10 sec. 'ON' (as with the series with a dark 10 sec. 'OFF' period), or level-off at about 3 or 4 sec. (i.e. level-off at the same point as that of transition in the level of the decay slope, assuming changes in decay slope were observed)? It is not clear, from the findings presented here, whether the critical integration periods underlying strength and decay slope are identical; or whether the neural modifications which underlie decay slope require a further undisturbed 2 or 3 sec. for full "consolidation". The experiments proposed would provide clarification on this point.

4. Several other questions are of interest with respect to the effect

of an interpolated period of diffuse achromatic illumination: (a) Would the same systematic changes be observed with lengthening of the 'ON' period, if the interstimulus period were less than 1 sec. and completely illuminated? Moreover, with interstimulus periods less than 1 sec., would there be a clear point at which the achromatic illumination has no effect? (b) More data are needed to confirm that establishment of the A/E is also impeded when the interpolated pulse occurs just prior to onset of the McCollough patterns. Further clarification is needed concerning the precise effects of moving an interpolated pulse from before to after coloured pattern stimulation. (c) Would the impeding effect show up dichoptically? (d) Under dichoptic conditions of presentation, would there be any differential effect of the period of illumination, depending on whether this occurred prior or subsequent to coloured pattern stimulation?

5. There is evidence that insertion of periods of patternless colour or achromatic gratings into the stimulation sequence, exert a much more substantial impeding influence than does a period of achromatic illumination (Appendix A: Murch, 1976). However, Appendix A only considered the effect in the context of dichoptic induction, while Murch (1976) did not use quantitative techniques in assessing A/E strength, or consider the influence of relative timings (e.g. before/after coloured pattern stimulation). The following questions are of some interest regarding the effect of other stimuli on induction of the McCollough Effect: (a) Would a random noise pattern have the same impeding effect as a period of diffuse illumination? (b) What are the critical time periods, and the extent of the disruptive influence of interpolated periods of exposure to achromatic gratings and diffuse colours? (c) Is the disruptive influence independent of relative timings of the different stimuli; or do these have

an important influence, and are there systematic differences in this respect between achromatic gratings and diffuse colour? (d) Do the orientation or colour of the interpolated stimuli have a differential effect relative to colour or orientation of the McCollough patterns? (e) Is there a critical period of separation of the interpolated and McCollough stimuli? If so, is it always about 1 sec. or does it vary depending on the critical time period required for these interpolated stimuli?

6. It has been suggested (Chapter 6) that when the dark 'OFF' period is 1 sec. or less, successive stimuli may be integrated even though they are dissimilar in both orientation and colour. To simplify the experimental conditions, it may be worthwhile using only one stimulus orientation and colour, and investigating the effect of varying the 'OFF' period, for a fixed 'ON' period. The question is whether similar systematic changes in strength will be observed with lengthening of the 'OFF' period, particularly over the range 0 to 3 sec.

7. Use of only one orientation and colour would provide the opportunity for better analogues of experiments utilising an achromatic grating and measuring elevation of visual thresholds. In view of some similarities in the time course of contingent and non-contingent A/E's, it may be appropriate to consider a more thorough investigation of elevation of thresholds following exposure to chromatic and achromatic gratings. Particular attention should be paid to the systematic manipulation of the various temporal parameters, and to measurements of the magnitude of the initial effect and the time course of recovery. This kind of study would provide more detailed information on the similarities and dissimilarities between the two forms of A/E, and on possible limitations

of the threshold elevation technique in studies of the time course of visual A/E's.

APPENDIX A:

TEMPORAL PARAMETERS OF STIMULATION AFFECT STRENGTH OF DICHOPTICALLY-INDUCED MCCOLLOUGH-TYPE AFTEREFFECTS

Introduction

In view of the importance for the theory of the McCollough Effect of establishing the mechanism of interaction of pattern and colour information in the visual system, the question arises as to how the strength of the A/E may be related to relative timing parameters of different features of the stimulus situation. In terms of the 'double-duty detector' theory, one might assume that the strength of the A/E would vary in relation to the time for which these units are supposedly being stimulated. That is to say, an A/E should only be built-up during the period of simultaneous presentation of pattern and colour. An A/E so established should not be affected as a result of preceding or subsequent stimulation by either feature alone, since different neural sub-populations are assumed to be involved in the processing of these features when they occur separately. Nor would one expect the relative duration of individual and simultaneous stimulation to affect A/E strength. The only factor which should affect A/E strength is the degree of temporal overlap of pattern and colour stimulation.

These questions may be considered in the context of dichoptic induction of the A/E. It has been shown that if an achromatic grating is presented to one eye while the other eye is simultaneously stimulated by a monochromatic (patternless) field, a weak McCollough-type A/E can be established in each eye (MacKay & MacKay, 1973; 1975). This technique provides a means of spatially separating the different features peripherally, so that any interactive effects observed may be assumed to occur at a central site. The questions we may consider is how the strength of an A/E induced by simultaneous presentation of two stimuli may be affected by manipulating the relative periods of presentation of the pattern and colour and by the relative onset and offset timings of the two features.

I report here the results of pilot experiments in this area. These indicate that temporal variables can critically affect the strength of dichoptically-induced McCollough-type A/E in ways not easily accounted for by the conventional theory of the mechanism of the pattern-contingent chromatic A/E.

Apparatus and Methodology

The apparatus and procedure for inducing and testing A/E strength are essentially as described in Chapter 2 of this thesis, but with the following modifications. Firstly, pre- and post- adaptation testing sessions were carried out in a blacked-out room. Secondly, subjects were required to make reports of the hue associated with the orientations of the test card before and after exposure to the adapting patterns, in addition to making a number of colour matches for each eye in turn.

During adaptation, one eye was exposed to a diffuse red field (590-670 nm) alternating with a diffuse green field (480-560 nm), while the other eye was exposed to alternating orthogonally oriented black and white gratings. Field sizes in the two eyes were identical and optically superimposed. Luminances were matched at approximately 0.6 LFL. Field illumination was electronically triggered. Exposure duration was 15 min. in all cases.

The effects on A/E strength of two variables of stimulation were considered: (1) the relative duration of stimulation of the two eyes, and (2) asynchronies in onset and offset timing of the two stimuli.

RESULTS

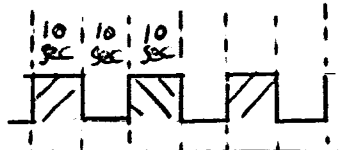
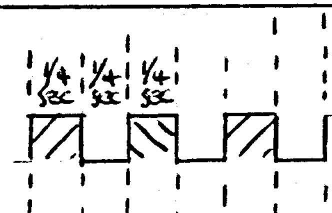
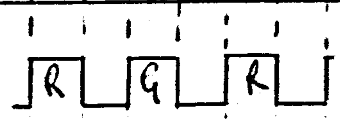
(1) Comparison of the effects of two sequences of stimulation

The purpose of these experiments was to investigate the effect on A/E strength of the absolute length of the 'ON' period. It was not possible to investigate this thoroughly, but a guide could be obtained by comparing two sequences, one with a short 'ON' (1/4 sec.) and one with a long 'ON' (10 sec.). For each sequence the length of the 'OFF' period was equal to the 'ON'.

The results for the two sequences used are shown in Table A:1. It can be seen that the results for the two subjects are similar. The main finding is that there is very little difference in strength related to the length of the 'ON' period. This is contrary to the finding for the ordinary McCollough Effect (see Chapter 4). Two other features of the results are in accordance with previous reports from this laboratory (MacKay & MacKay, 1973; 1975): the A/E strength is greater in the eye previously exposed to achromatic pattern stimuli, and the polarity of the A/E is opposite between the two eyes (see also Mikaelian, 1975). This difference in polarity between the eyes is characteristic of other results to be reported and will not be explicitly mentioned again.

All further experiments to be reported in this section will be compared with those for the 10 sec. 'ON'/10 sec. 'OFF' sequence. This sequence was chosen for comparison purposes because it provides ample scope for variation in relative onset and/or offset asynchrony of the stimuli to the two eyes, and for variation in the length of the period of exposure of one or other of the two stimuli.

TABLE A:1

Stimulation	Temporal Sequence	SRH		JPM	
		Strength	Polarity	Strength	Polarity
(i) Pattern Stimulated eye (10 sec.)		1.1_4	Same	1.1_3	Same
Colour Stimulated eye (10 sec.)		0.2	Comp	0.3	Comp
(ii) Pattern Stimulated eye (¼ sec.)		0.8_1	Same	1.0_1	Same
Colour Stimulated eye (¼ sec.)		No A/E		0.6	Comp

(2) Varying the period of one stimulus feature relative to the period of the other

The purpose of these experiments was to investigate the effect of reducing the period of one stimulus relative to the period of the other, while maintaining simultaneous onset of stimulation of the two eye channels. For comparison purposes, one of the stimuli had a presentation period of 10 sec. The series of experiments is shown in Table A:2, the results for the 10 sec. 'ON' and 10 sec. 'OFF' are included again so as to make the table complete.

It can be seen from this table that reducing the period of presentation of the coloured field to 5 sec. while the period of the pattern stimulus is maintained at 10 sec. has a quite substantial effect on the strength of A/E (ii). For one subject the eye that had previously been stimulated with the achromatic grating has the strength reduced by about 80% relative to that for the 10 sec. 'ON'/10 sec. 'OFF' sequence. For the other subject the A/E is abolished completely. For both subjects, there is no measurable A/E for the colour stimulated eye, compared with a very small A/E under conditions of equal periods of stimulation of the two eyes.

However, when the situation is reversed and the duration of the pattern stimulus is reduced while colour stimulation is maintained at 10 sec., the effect on the strength of A/E is not so dramatic. Comparing (i) with (iii) it can be seen that for the pattern stimulated eye the A/E strength is hardly affected for two of the subjects, while for the other two it is reduced by about 50%. For the colour stimulated eye the small A/E on condition (i) is abolished for three of the subjects and reduced for the fourth. Reduction in the duration of either the pattern or colour stimulus to one sec. (conditions (iv) and (v)) resulted in no measurable

TABLE A:2

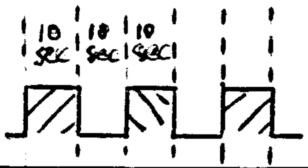
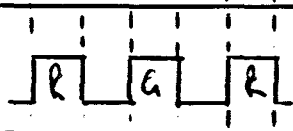
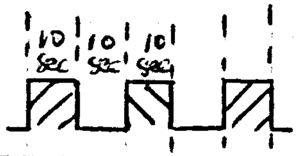
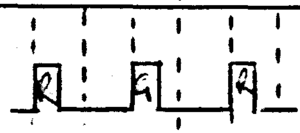
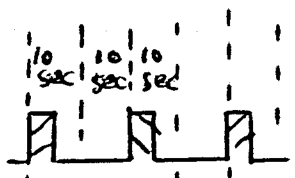
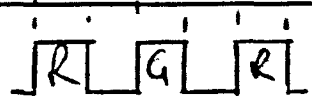
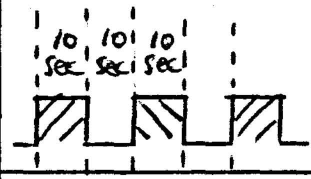
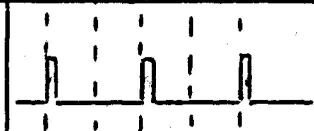
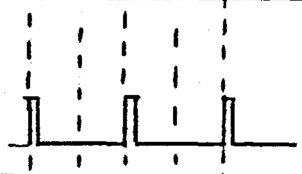
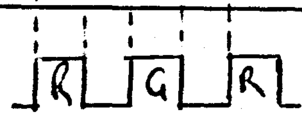
Stimulation	Temporal Sequence	SRH		JPM		VM		RM	
		Strength	Polarity	Strength	Polarity	Strength	Polarity	Strength	Polarity
(i) Pattern Stimulated eye (10 sec.)		1.1 $_{4}$	Same	1.1 $_{3}$	Same	0.7 $_{2}$	Same	1.3 $_{1}$	Same
Colour Stimulated eye (10 sec.)		0.2	Comp	0.3	Comp	0.6	Comp	0.4	Comp
(ii) Pattern Stimulated eye (10 sec.)		0.2 $_{1}$	Same	No A/E					
Colour Stimulated eye (5 sec.)		No A/E $_{1}$		No A/E					
(iii) Pattern Stimulated eye (5 sec.)		0.9 $_{1}$	Same	0.5	Same	0.7 $_{1}$	Same	0.8 $_{1}$	Same
Colour Stimulated eye (10 sec.)		No A/E		No A/E		0.3	Comp	No A/E	Comp

TABLE A:2 (contd.)

Stimulation	Temporal Sequence	SRH		JPM		VM		RM	
		Strength	Polarity	Strength	Polarity	Strength	Polarity	Strength	Polarity
(iv) Pattern Stimulated eye (10 sec.)				No A/E					
Colour Stimulated eye (1 sec.)				No A/E					
(v) Pattern Stimulated eye (1 sec.)				No A/E					
Colour Stimulated eye (10 sec.)				No A/E					

the strength of the associated A/E.

(3) Effect of delay of onset timing of pattern stimulation

The next series of experiments varied the timing of presentation of the stimulus to one eye relative to the timing of presentation to the other. To enable comparison with previous results, one stimulus again had a fixed 'ON' duration of 10 sec. and the other had a duration of 5 sec. (To have both stimuli on for 10 sec. and vary relative timing would have involved varying either the 'OFF' duration or the cycle time, and this would have made it difficult to make direct comparison with previous results.) The independent variable in this set of experiments was therefore the 'location' of the shorter duration stimulus within the 'time frame' of the other. In this way it was possible to keep the durations constant and similar to previous conditions, and vary only the relative onset and offset timings.

Since reduction in the duration of the colour stimulus to 5 sec. was associated with abolition of the A/E, experiments were restricted to the situation in which the coloured field was illuminated for 10 sec. and the patterned field for 5 sec. The immediate question was whether delaying the onset of the pattern stimulus would be associated with any change in the strength of A/E compared with condition (iii) of Table A:2. The results can be seen in Table A:3. Condition (i) is A:2(iii) repeated for ease of comparison. Condition (ii) shows the effect of delaying the onset edge by 5 sec. - that is, so that the offsets are simultaneous. It can be seen that there is a substantial reduction in the strength of A/E in the eye having received pattern stimulation. For one subject the A/E is abolished completely, while for the other two it is reduced by about 30%. For two of the subjects there was no measurable A/E in the colour stimulated

TABLE A:3

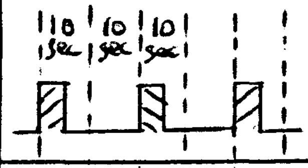
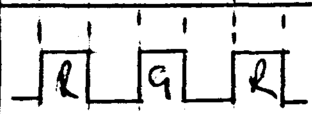
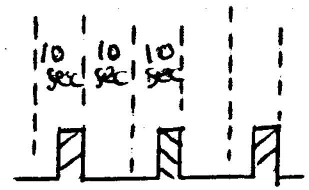
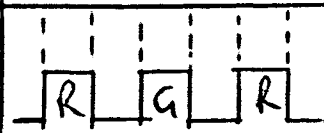
Stimulation	Temporal Sequence	JPM		VM		RM	
		Strength	Polarity	Strength	Polarity	Strength	Polarity
(i) Pattern Stimulated eye (5 sec.)		0.9[1]	Same	0.7[1]	Same	0.8[1]	Same
Colour Stimulated eye (10 sec.)		No A/E		0.3	Comp	No A/E	
(ii) Pattern Stimulated eye (5 sec.) Onset delay 5 sec.		No A/E[1]		0.2[1]	Same	0.3[1]	Same
Colour Stimulated eye (10 sec.)		No A/E		0.3	Comp	No A/E	

TABLE A:3 (contd.)

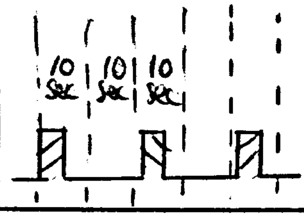
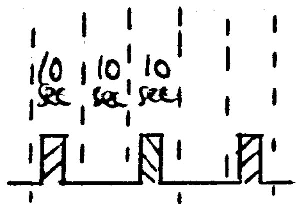
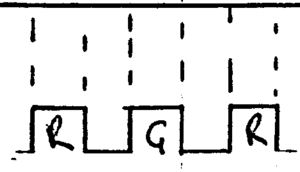
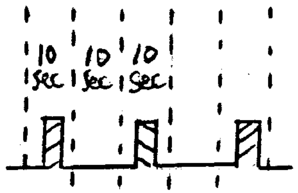
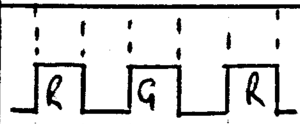
Stimulation	Temporal Sequence	JPM		VM		RM	
		Strength	Polarity	Strength	Polarity	Strength	Polarity
(iii) Pattern Stimulated eye (5 sec.) Onset delay 1 sec.				0.6 [1]	Same	0.6 [1]	Same
Colour Stimulated eye (10 sec.)				0.5	Comp	No A/E	
(iv) Pattern Stimulated eye (5 sec.) Onset delay 2 sec.		0.8 [1]		1.1 [1]	Same	0.5 [1]	Same
Colour Stimulated eye (10 sec.)		No A/E		0.6	Comp	0.3 (not visible)	Comp

TABLE A:3 (contd.)

Stimulation	Temporal Sequence	JPM		VM		RM	
		Strength	Polarity	Strength	Polarity	Strength	Polarity
(v) Pattern Stimulated eye (5 sec.) Onset delay 3 sec.		0.5		No A/E	Same	0.4	Same
Colour Stimulated eye (10 sec.)		No A/E		No A/E?	Comp	No A/E	

eye for either condition, while for the third subject it was identical under the two conditions.

This result would tend to implicate the onset as the critical variable. It will be remembered, comparing conditions A:2(i) and (iii), that reducing the duration of the pattern stimulation to 5 sec., making the offset of the stimuli asynchronous, had very little effect on the strength of the A/E. However, when a similar reduction in duration is made by 'shifting' the onset edge, the strength is markedly lower. This reduction must therefore be associated with the onset asynchrony.

The question then arises as to whether the strength of A/E will decrease steadily if this onset edge were moved gradually from zero delay to 5 sec. delay or whether there is a 'critical' duration, in which case the A/E strength should not decline until this 'critical' duration is exceeded. The effect of delaying the onset of the pattern stimulus by 1, 2 and 3 sec. can be seen in conditions (ii), (iii) and (iv) shown in Table A:3. Unfortunately, the results are equivocal with respect to these questions. For two of the subjects there is little change for the pattern stimulated eye as the delay is increased from zero to two sec., and then the A/E strength falls-off fairly sharply. For the other subject there is a steady decline in strength. Two of the subjects show no measurable A/E in the colour stimulated eye under any of the conditions. The third subject shows the same sequence of changes as in the pattern stimulated eye.

(4) <u>Effect of reducing the duration of the coloured stimulus</u>

The results of condition A:2(ii) show that when the duration of the coloured stimulus is reduced to 5 sec. by variation in the relative offset of the stimuli, there is a marked reduction in the strength of the associated A/E. A similar question arises to that considered in the last section. If the duration of the coloured stimulus is reduced steadily from 10 sec. by increases in the offset delay, will the strength of A/E decrease progressively or will there be a 'wiping out' effect at some critical offset asynchrony?

This problem was investigated briefly on one subject. The results are shown in Table A:4, condition (i) being a repeat of A:2(i). It can be seen that as the duration of the coloured stimulus is reduced from 10 sec. to 9 sec., so that there is a 1 sec. offset asynchrony, the strength in the pattern stimulated eye remains unchanged, but the strength in the colour stimulated eye is reduced quite markedly. When the offset asynchrony is increased to 2 sec. the strength of A/E in the pattern stimulated eye now falls off quite sharply while the strength in the colour stimulated eye is not affected any further. Increasing the gap to 3 sec. has no further measurable effect on the strength in either eye. These results would suggest that the strength can be most critically affected with offset asynchrony of about 1 or 2 sec.

The parallel series of experiments, in which the duration of the pattern stimulus was systematically reduced, were not completed due to lack of time.

TABLE A:4

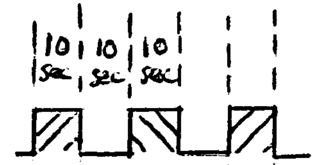
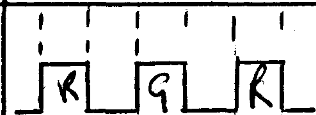
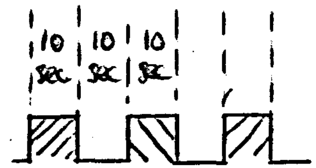
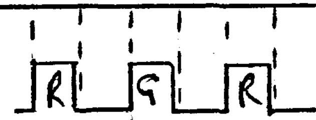
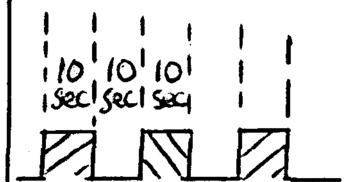
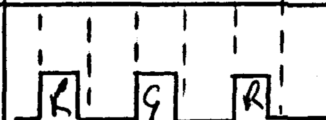
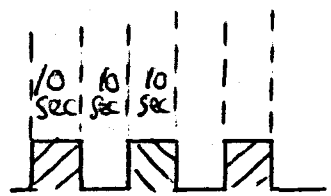
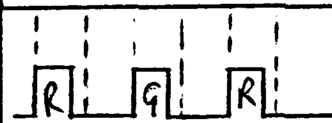
Stimulation	Temporal Sequence	VM	
		Strength	Polarity
(i) Pattern Stimulated eye (10 sec.)		0.7 2	Same
Colour Stimulated eye (10 sec.)		0.6	Comp
(ii) Pattern Stimulated eye (10 sec.) Offset delay 1 sec.		0.6 1	Same
Colour Stimulated eye (9 sec.)		0.1	Comp

TABLE A:4 (contd.)

Stimulation	Temporal Sequence	VM	
		<u>Strength</u>	<u>Polarity</u>
(iii) Pattern Stimulated eye (10 sec.) Offset delay 2 sec.		0.2	Same
Colour Stimulated eye (8 sec.)		0.2	Comp
(iv) Pattern Stimulated eye (10 sec.) Offset delay 3 sec.		0.2	Same
Colour Stimulated eye (1 sec.)		0.3	Comp

Discussion

In the first series of experiments it was shown that when short 'ON' and 'OFF' durations were used, very similar intensities of A/E were obtained to those associated with longer durations. This suggests that over a fairly wide range of values the absolute timing parameters are probably not critical. The reduction in strength of A/E when the duration of one of the stimuli is shortened is therefore much more likely to be due to the change in the relative durations of the two stimuli. The implication would seem to be that if activity is maintained in one eye channel for some period after cessation of stimulation of the other, the result may be a 'wiping out' of the A/E (presumably) built up during the preceding period of simultaneous stimulation of the two eyes.

An example may help to make this clearer. Suppose that activity is simultaneously set up in the two eye channels, with pattern being presented to the left eye and colour to the right. While both stimuli are illuminated, there will be interaction between the eye channels and a 'transfer' of information, and at some level a process of adaptation will be taking place to both stimuli. After 5 sec. the colour stimulus is turned off, leaving only the achromatic pattern visible in one eye channel, with darkness in the other. We can infer from previous work on transfer of A/E in general that the pattern information will continue to be transferred at some level to the other eye channel, and so a new process of adaptation should be set up to only one stimulus feature (Blakemore & Campbell, 1969). The present results show that if the pattern stimulus is on alone for a sufficient length of time (of the order of 2-3 sec.) this second adaptive process will somehow 'wipe out' the effects of the preceding period of exposure to two stimuli.

In the converse situation, in which the duration of the pattern stimulus is shortened relative to the duration of the colour, the decrease in the strength of the A/E is not so marked. This may perhaps imply that the 'wiping out' effect of the colour alone is not as great as that of pattern alone.

The present experimental results are perhaps an analogue of those described by Skowbo et al (1974). They showed that exposure to achromatic gratings shortly after adaptation to McCollough patterns was associated with a faster rate of decay of the A/E compared with that associated with normal visual stimulation in the post adaptation period. Moreover, exposure to homogeneous chromatic fields was not associated with this increased rate of decay of the A/E. Skowbo's results therefore provide evidence for selective interactive effects between features of the adaptation and post-adaptation environment. The present results indicate that these interactive effects can occur between different stimulus features within the adaptation period.

The present results are equivocal with respect to the question of the rate of decline in strength associated with reduction in duration of one or other of the stimuli. The results for two of the subjects are more suggestive of a steady decline in strength as the duration of the pattern is progressively shortened, while the limited results from the other two subjects are not consistent with this interpretation. The results for the one subject show a marked decrease in strength when the duration of the coloured stimulus is reduced beyond one or two seconds with respect to the duration of the patterned stimulus.

A similar problem arises in the interpretation of the results involving variable onset timing asynchronies between the two eyes. The results for two of the subjects show a fairly sharp decrease in the strength of the A/E as the onset asynchrony is increased beyond two or three seconds. The third subject shows a steady decline in strength with increase in asynchrony.

However, the fact that the strength of A/E does clearly vary with onset asynchrony is itself of considerable interest. Results along the same lines have been reported by Murch (1976) for the normal McCollough A/E. He has shown that if the onset of the colour is delayed by 1 sec. or more relative to pattern onset (with simultaneous offset), the strength of A/E is reduced from that for simultaneous onset. Murch does not indicate how accurately presentation times and delays could be controlled with the use of a slide projector, but the timing values reported as critical are comparable with those presented here.

One possible explanation is analogous to that proposed earlier, and assumes that prior exposure to a single stimulus feature may set up activity which cannot be effectively 'overwritten' by the conjoint effect of the subsequently presented pattern and colour. Further, the present results would tend to suggest that the colour alone has a greater effect when it occurs prior rather than subsequent to simultaneous stimulation by pattern and colour. Murch (1976), although chiefly concerned with the effect of delaying the pattern stimulus, does report that A/E are weaker if the pattern is delayed by half a second compared with delay of the colour for a similar period. This suggests that colour alone can have a greater effect than pattern when they occur prior to simultaneous presentation of pattern and colour. I have previously suggested that pattern alone can have a greater 'wiping out' effect when it occurs subsequent to simultaneous presentation. It may well be that pattern alone and colour can affect the system to different degrees, depending on the temporal arrangement of the stimuli. This question requires further investigation.

APPENDIX B:

INTERACTION BETWEEN EYE CHANNELS DURING INDUCTION OF PATTERN-CONTINGENT CHROMATIC AFTEREFFECTS

Introduction

If only one eye is exposed to the entire stimulus in an adaptation experiment, or each eye is exposed to only a part of the total stimulus configuration, and on subsequent testing both eyes show an A/E, then two things may be clearly inferred. Firstly, the site of the adaptation effect is post-retinal. Secondly, interaction has occurred between the eye channels at some level(s). Psychophysical studies have now established that the A/E of movement (Barlow and Brindley, 1963), tilt (Campbell and Maffei, 1971), orientation (Gilinski and Doherty, 1969; Blakemore and Campbell, 1969) and size (Blakemore and Sutton, 1969) show this transfer effect to the eye unexposed to the adapting stimulus. Barlow and Brindley (1963) have confirmed that the site of adaptation must be post-retinal by showing that pressure blinding the exposed eye immediately after adaptation does not prevent transfer, though pressure blinding before adaptation does.

Two lines of evidence have been taken to support the idea that the site of adaptation and the site of binocular interaction are in fact one and the same. Firstly, the size of the A/E in the non-adapted eye is quite substantial, but usually does not exceed 80% of that in the eye exposed to the patterns (Gilinski and Doherty, 1969; Blakemore and Campbell, 1969). Secondly, the characteristics of the A/E are usually the same in the non-adapted eye as in the adapted eye - e.g. the angular selectivity is the same (Gilinski and Doherty, 1969). By analogy with results from single unit studies of cat (Hubel and Wiesel, 1962) and monkey (Hubel and

Wiesel, 1968) striate cortex, it has been assumed that binocularly driven units sensitive to the orientation of a contour may exist in the human visual cortex and may be the site of both binocular interaction and adaptation. Persuasive support for this idea has been provided by studies of patients who lack stereoacuity. These subjects do not show interocular transfer of either the tilt (Mitchell & Ware, 1974) or motion (Mitchell, Reardon & Muir, 1975) A/E. Stereoacuity was independently assessed in both cases. Moreover, the degree of transfer for normal subjects varied in relation to their measured stereoacuity (Mitchell, Reardon & Muir, 1975).

The total absence of transfer of the pattern-contingent chromatic A/E (McCollough, 1965) indicated that for this A/E the site of adaptation could not be at the level of binocularly driven units. It has been assumed that adaptation must occur at the level of edge-detectors in the uniocular pathway (Coltheart, 1973; Over et al, 1973).

There are a number of difficulties concerning the assumption that adaptation and binocular interaction occur entirely at the same site. Firstly, if only a single class of units is involved one would expect transfer to be complete. So far as I know, there is only one report of complete transfer of an A/E (Campbell & Maffei, 1972). As Andrews (1972) has pointed out, partial transfer of effects are a difficult category to account for. Secondly, Hubel & Wiesel (1962; 1968) classified cells into a number of groups depending on degree of monocular dominance. A few cells can be driven by stimulation of one eye only, and not by stimulation of the other eye. Another small group of cells can be driven only by simultaneous stimulation of both eyes. However, the majority can be driven by stimulation of one eye or the other, though the two eyes may not be equally effective. It is not clear which class of cells may underlie partial transfer effects. Finally, it has been shown that if diffuse colour is presented to one eye and an achromatic grating to the other, McCollough-type A/E can be induced in both eyes (MacKay & MacKay, 1973; 1975), the polarity of A/E in one eye being opposite to that in the other. This latter finding provides evidence for transfer of information between eye channels at a site prior to that at which adaptation takes place. In other words, there may be interocular interaction distinct from transfer of adaptation effects.

A systematic study was undertaken to consider both the question of interaction between eye channels and full transfer of adaptation effects. In this study, one eye was always exposed to McCollough patterns, while the other eye was exposed to one of six possible conditions. The conditions for the non-adapted eye were as follows. First, total occlusion. Second, diffuse achromatic illumination. Both conditions were aimed to detect full transfer of both features of the adapting patterns. Third, achromatic grating of orthogonal orientation to that simultaneously present in the other eye channel. Fourth, achromatic grating with the same orientation as that simultaneously present in the other eye channel. Any A/E in the non-adapted eye would indicate transfer of colour information. Any differences in the strength of A/E between conditions three and four may indicate interaction at the level of contour processing. Fifth, diffuse colour, the same colour being presented simultaneously to the two eyes. Finally, diffuse colour, opponent colours being presented simultaneously. Any A/E in the non-adapted eye would indicate transfer of pattern information. Any difference between conditions five and six would indicate interaction of the colour features, which could be at a site prior to that at which contour processing becomes important.

The results to be reported provide further evidence for interocular interaction in the colour domain, though full transfer effects are absent.

Methodology

The apparatus and adapting procedure were similar to that described in Chapter 2. The fields of the tachistoscope were arranged so that one eye could be stimulated by a coloured grating pattern, red alternating with green, while the other eye was simultaneously exposed to one of six possible conditions. Field sizes in the two eyes were identical and optically superimposed, giving the appearance of a single square field. The intensity of the white and coloured stripes of the grating pattern, and of the diffuse white and coloured fields, were equated at approximately 0.6 LFL. Two fields were triggered such that both eyes were stimulated simultaneously and for equal periods. The stimulation sequence was 10 sec. 'ON'/0 sec. 'OFF' repeated for 15 minutes.

There were six possible conditions for the eye not exposed to the McCollough patterns. (1) total occlusion, (2) diffuse achromatic illumination, (3) achromatic grating, similar orientations being paired in the two eyes, (4) achromatic grating, orthogonal orientations being paired, (5) diffuse colour, similar colours being paired, and (6) diffuse colour, opponent colours being paired. In condition (1) an eye patch was worn over the non-adapted eye to ensure total exclusion of any stray light.

At the end of adaptation the room lights were switched on* and the subject moved quickly to test the apparatus and made a subjective report of the appearance of the test-card, for the non-adapted eye only. This whole procedure typically took less than 1 min. The strength of the A/E was then measured in the way already described (Chapter 2).

*N.B. A better procedure would have been to keep the room blacked out: see Appendix A.

Three subjects were exposed to all conditions, the order for two of the subjects being arranged in pseudo random fashion. The series was completed first on K.B., the order of exposure to conditions being as reported in the results section. All experiments were carried out at approximately the same time of day, between December 1974 and February 1975. For one subject, each condition was repeated at least once, with the second presentation reversing stimuli between eyes. The orientation and colour pairings of the McCollough patterns were constant throughout for this subject. This allowed a check to be made for any consistent differences between the eyes. The second subject was similarly exposed to a constant orientation and colour pairing for the McCollough patterns which were presented to the same eye on all occasions. For the third subject, no particular order of presentation was adopted.

Since a substantial A/E was generated in one eye, which involved the subject putting a large colour bias on the centre 'window' of the test card, it was necessary to ensure that this bias itself could not give rise to a small A/E in the non-adapted eye. The following control procedure was carried out independently of the experimental conditions. The subject, assumed to have no orientation linked colour bias, made the normal pre-test 'neutral' settings. No A/E was measurable at this stage. The right eye was then exposed to maximum colour bias while fixating the centre of one window for approximately 5 seconds (which was an average time for a reading for this subject). The right eye was then occluded by means of the movable eye-patch and with the left eye exposed this bias was taken off and a normal setting to neutral was made. The right eye was then exposed again with the left occluded and the maximum colour bias put on in the opposite direction while the subject fixated for 5 seconds the window with the orthogonal orientation. The eye patch was changed over again and the subject immediately made a setting for the left eye, for the same orientation just fixated by the right eye. This procedure was repeated four times. Both eyes were then tested in the normal way. There was no measurable difference in settings between the eyes, and no indication of an orientation-linked colour A/E in the settings made or subjective report of the appearance of the achromatic part of the test card. We can conclude that brief exposure to colour bias on the window of the test card does not induce any measurable or visible A/E.

As a further control in the experimental context, subjects returned the window bias to approximately neutral after making a setting with the eye which had been exposed to the McCollough patterns. This ensured that the eye not exposed to McCollough patterns did not receive orientation-linked colour stimulation.

TABLE B.1

CONDITION	SUBJECT KB				SUBJECT SRH				SUBJECT MY			
FOR NON-ADAPTED EYE	NON-MCCOLLOUGH ADAPTED EYE			MCCOLLOUGH ADAPTED EYE	NON-MCCOLLOUGH ADAPTED EYE			MCCOLLOUGH ADAPTED EYE	NON-MCCOLLOUGH ADAPTED EYE			MCCOLLOUGH ADAPTED EYE
	STRENGTH	SUBJ. RPTS.	POLARITY	STRENGTH	STRENGTH	SUBJ. RPTS.	POLARITY	STRENGTH	STRENGTH	SUBJ. RPTS.	POLARITY	STRENGTH
Dark	0.2 NS	V NV	0 /	$\bar{X}$=4.9 4.6 5.1	NS	NV	/	NM	NS	NV	/	NM
White	0.2 NS	V NV	S /	NM 40	NS	NV	/	5.2	NS	NV	/	NM
Black and white gratings. Same orientation in the two eyes	$\bar{X}$=0.9 0.7 1.0 1.0	NV V V	0 0 0	$\bar{X}$=3.5 3.4 3.0 4.0	0.6	V	0	4.2	1.7	V	0	NM
Black and white gratings. Opposite orientations in the two eyes	0.4 0.5 0.7	NV V V	S S S	$\bar{X}$=3.3 4.2 3.4 2.2	0.5	V	S	3.4	0.8	V	S	NM
Diffuse colour. Same colour in the two eyes	$\bar{X}$=0.4 0.4 0.6 0.3	V V V	S S S	$\bar{X}$=3.2 2.6 3.5 3.5	0.6	V	S	4.0	0.3	V	S	4.2
Diffuse colour Opponent colours in the two eyes	NS 1.0	NV NV	/ 0	NM 3.9	0.2	NV	0	NM	0.2	NV	0	NM

NV = Not visible NM = Not measurable NS = Not significant S = Same 0 = Opposite V = Visible

Results

No differences were found with respect to eye preference when conditions were reversed between eyes and so results are pooled for subject K.B. In all cases the polarity of the A/E was in the expected direction. The polarity of the A/E - if one was induced - in the other eye is designated as either the 'same' or 'opposite' with reference to the direction of the A/E in the McCollough adapted eye. A/E strength of 0.1 or less is regarded as not significant (NS). Subjective reports indicate whether the A/E is 'visible' (V) or 'not visible' (NV). The results are summarised in Table B:1 and are discussed according to stimulus conditions for the non-McCollough adapted eye.

(1) Dark

These experiments were conducted in order to confirm previous reports (not using an objective measuring technique) that interocular transfer of the A/E does not occur. They also provide a baseline with which to compare the other conditions.

It can be seen that there is no evidence for transfer of the A/E. On the one occasion for subject K.B. on which there was a measured effect, no colour A/E was subjectively visible. On all occasions a substantial A/E was generated in the eye exposed to the McCollough patterns, going beyond the range of the measuring apparatus for two of the subjects.

(2) Diffuse white light

The results are very similar to those discussed in the last section. An A/E could be measured on only one occasion for subject K.B. but it was not subjectively visible. On all other occasions for all three subjects there was no measurable A/E and no subjective report of colours associated with the achromatic test orientations. Again, substantial A/E were generated in the eye exposed to McCollough patterns.

(3) Black and white gratings with the same orientation paired with McCollough pattern orientation

It can be seen that on all occasions an A/E was measurable in the eye having received achromatic pattern stimuli. On only one occasion, for subject K.B., the A/E was not subjectively visible. Again the normal A/E was quite clear and of reasonable strength in the eye exposed to McCollough patterns, though for two of the subjects the measured strength was not as great as for the previous two conditions.

The polarity of the A/E in the McCollough-adapted eye is in the direction expected. For all subjects the A/E is in the opposite sense in the eye previously exposed only to achromatic gratings, and there is full agreement between the measured and reported directions.

(4) Black and white gratings with orientation paired orthogonally to that of the McCollough pattern

The results are similar to those in the previous group with a clear A/E measurable in the eye exposed to achromatic patterns and subjectively visible on all but one occasion (for subject K.B). For two of the subjects the measured A/E is smaller than in the previous condition; for the other subject there is very little difference between the two conditions. Strength of the A/E in the McCollough-adapted eye are very similar to those in the previous condition.

Again, the polarity of A/E is in the direction expected in the eye having received McCollough adaptation and on all occasions the polarity of

A/E is in the same sense in the other eye.

(5) <u>Diffuse colour: Colour pairings same between the two eyes</u>

An A/E was subjectively visible and could be measured on all occasions in the eye previously exposed to patternless colour stimulation. For two of the subjects the strength is very similar to the previous condition, in which a black and white grating was presented with orientation opposite to that simultaneously presented to the other eye; for the third there is a slight decrease. There is very little change in strength in the eye having received stimulation by the McCollough patterns. The polarity of A/E is as expected in this eye, and is in the same direction in the eye exposed to diffuse colour.

(6) <u>Diffuse colour: Colour pairings opposite between the two eyes</u>

For two of the subjects the measured A/E is very small and there are no subjective reports of apparent colour on the test card, for the eye exposed to diffuse colour. For the third subject there was no visible or measurable A/E on one occasion, though on the other occasion an A/E could be measured which was not subjectively visible. With respect to this latter result, for subject K.B. an A/E of this measured magnitude was usually distinctly visible on the test card. This is a puzzling result. However, the polarity of A/E indicated by the measurement of strength are clearly in agreement with that for the other two subjects, indicating that the direction is opposite between the two eyes. On all occasions a large A/E was measured in the McCollough adapted eye.

<u>Some further experiments related to the question of initial strength when only one eye adapted</u>

The problem of comparing results in terms of initial strength was made difficult by not having rigorous control over the time in normal illumination prior to the first reading. The results for subjects K.B. and S.R.H., shown in Table B:1, raise the possibility that the initial strength may be greater on conditions 1, 2 and 6. In order to assess whether the differences are correlated with stimulus conditions, or simply related to the time in normal room illumination, monocular and binocular stimulation for the same sequence were compared. The subject was exposed to normal room illumination for exactly 1 minute before taking the first post-adaptation reading. The results for K.B. are shown in Table B:2. Mrs. V. MacKay had also considered this question independently, and I am grateful for permission to include her results. It can be seen that there is no significant difference between the conditions so we may conclude that the differences shown in Table B:1 are random variations.

<u>Opposite McCollough patterns presented to each eye</u>

In view of the demonstrated interaction between eye channels associated with certain stimulation conditions, the question arose as to whether a difference in strength could be measured between eye channels when opposite coloured gratings were presented simultaneously to the two eyes. There are four possible pairing conditions:

1. Colour and orientations are the same in the two eyes
2. Orientations are the same but colours opponent
3. Colours are the same but orientations orthogonal
4. Both orientation and colour are different.

For these experiments, post adaptation procedure was identical to that described in Chapter 2 for the parametric study. It seemed unlikely that any obvious difference would be found for three reasons. Firstly, it has been shown that dichoptically induced and transfer effects are only

Table B:2. Strength of A/E following Monocular and Binocular stimulation

Subject	Date	Adaptation Condition				
		Monocular		Binocular		
		Left eye	Right eye	Left eye	Right eye	Average
K.B.	22. 4.75		3.5			
	4.12.74			3.6	3.1	3.4
	10. 2.75			2.9	2.8	2.9
V.M.	5. 9.74	3.4				
	9. 9.74		2.8			
	2. 9.74			3.5	3.4	3.5
	7.11.74			3.5	2.8	3.2

Table B:3

	Left eye	Right eye	Left eye	Right eye	Left eye	Right eye	Left eye	Right eye
	G ↖	R ↗	R ↖	R ↗	G ↗	R ↗	R ↗	R ↗
	R ↗	G ↖	G ↗	G ↖	R ↖	G ↖	G ↖	G ↖
Strength	2.9	3.7	3.5	2.4	4.2	2.5	3.6	3.3
Decay Slope	-0.28	-0.34	-0.28	-0.32	-0.29	-0.49	-0.57	-0.37

small and are therefore likely to be swamped by the comparatively greater strength of the normal A/E. Secondly, there is usually some amount of scatter in the values for decay slope and strength for different runs on the same sequence (see main results section) which makes it more difficult to be certain whether any small differences are related to the experimental conditions. Finally, measured strength and decay slope often differ between eyes even for a normal adaptation condition.

The results are shown in Table B:3. This contains the results of one experiment on each of the four conditions for one subject. There are clearly differences between eyes in terms of strength. Inspection of the results which form the basis of the temporal interaction matrix gives the impression that differences in strength between eyes were commonly of the order of 0.5 or less, but differences up to 1.0 were not uncommon; anything much higher than that was rare. The only one to fall outside this range is that in which the orientations are the same but colours are opponent for simultaneous presentations. However, the difficulty with drawing general conclusions is that on two occasions one eye shows a higher strength and on the other occasions the other eye. In the case of the decay slope the split is 3 to 1. There is a substantial difference even when the pattern and colour are the same to each eye. If this technique were to reveal any differences, it would need substantially more data than is presented here.

Discussion

There are four lines of evidence which, taken together, clearly lead to the conclusion that there is no interocular transfer of the McCollough Effect. Firstly, when one eye has light totally excluded while the other eye is exposed to the alternating coloured patterns, no significant A/E can be measured in the previously occluded eye and there are no subjective reports of colours associated with the orientations of the achromatic test pattern. This finding is in keeping with previous reports that colour 'fringes' associated with the wearing of prismatic spectacles do not transfer to the non-adapted eye, though disturbances of eye-hand co-ordination and spatial relationships do transfer (Hajos and Ritter,1965), that the colour-contingent tilt A/E does not show transfer effects (Shattuck and Held, 1975), and that testing for both features, the size (Murch, 1972) and tilt (Lovegrove and Over, 1973) A/E transfer, but the colour specificity is maintained only in the monocular condition.

Secondly, no A/E is measurable when the non-adapted eye is exposed to diffuse white light simultaneously with adaptation of the other eye. This confirms a previous negative finding (Over, Long and Lovegrove, 1973 (a)), but in this latter report only brief (100 msec.) stimulus presentations were used, which may only be adequate in inducing very weak A/E in the adapted eye itself (see main results section of this thesis). Therefore, it is not a sufficient condition for inducing pattern and colour transfer if the other eye channel is simply 'activated' by patternless white light, stimulation occurring synchronously with the adapting patterns. Sharpe (1974) does find transfer effects when measurements are made by threshold elevation techniques testing on colour gratings (see later).

Thirdly, when opposing patterns are presented simultaneously to the two eyes, there is no convincing evidence for a significant difference in strength between eye channels related to orthogonal patterns, opponent colours or both, compared with the measured strength when both eyes are exposed simultaneously to the same orientation and colour. This line of evidence is only suggestive, in that one cannot draw conclusions of "no transfer" from experiments which show that each eye can be adapted independently of the other. It may be, for example, that transfer effects are small and are therefore swamped by the effects of the adapting stimulus in the eye channels to which transfer has occurred, or opponent effects may be signalled in the other eye. McCollough (1965) failed to find transfer in a situation in which first one eye was adapted and then the other, a brief testing period separating the two adaptation periods.

Shattuck and Held (1975), in a report published subsequent to completion of the experiments presented here, make a similar claim of no transfer effect for the colour contingent tilt A/E. They report no significant quantitative differences in strength between the two eyes when each is adapted in an opposing way to the other, or compared with the magnitude of the effect when only one eye is adapted. They also show that stereo illusion effects can be generated based on opposite effects in the two eyes. Their results provide additional support for the data presented here.

Finally, the measured strength of the A/E in the eye exposed to the McCollough patterns is not affected by the presence or absence of stimulation of the other eye. A similar finding has been reported for the tilt A/E (Shattuck and Held, 1975).

Although interocular transfer of the A/E does not occur, there is clear evidence for interaction between eye channels at some level. An A/E can be measured and is subjectively visible in the eye exposed to achromatic gratings, which is indicative of a transfer of colour information. In terms of the size and polarity of the A/E in this eye, the results are consistent with those in which dichoptic induction techniques are employed (MacKay and MacKay, 1973; 1975; Mikaelian, 1975) (Over et al (1973) failed to find evidence for dichoptic induction of McCollough type A/E).

However, one would expect that the pattern component would also transfer, so the question of real interest is whether there is any evidence of interaction resulting from the presence of orthogonal orientations in the two eyes. Any interactive effects may reveal themselves in differences in strength between conditions in which the same or orthogonal gratings are simultaneously presented to the two eyes. The results for these conditions show only slight differences in strength for two of the subjects for the eye having received achromatic pattern stimulation, though for the third subject the strengths for the two conditions differ by a factor of two. In all cases the strength is lower when the orientations are opposite between the two eyes. If pattern information is transferred correctly (MacKay and MacKay, 1973; 1975) the results are in the direction indicative of only limited interaction at a level at which orientation parameters are important. The difference could be related to facilitation (when the orientations are the same) or inhibition (when they are orthogonal).

A/E strengths in the eye exposed to McCollough patterns are generally too large for one to expect to detect the (presumably) small transfer effects, if they exist at all. Moreover, there is no evidence for any significant differences in strength related to orientation features when both eyes are exposed to coloured gratings and the colours are the same in the two eyes.

On the basis of the reports by MacKay and MacKay (1973; 1975) one would also expect the pattern features to transfer to the eye receiving only diffuse colour illumination. However, in this situation the question of real interest is once again whether the strength of any induced A/E will be affected by the common colour features. The question is whether the polarity of the A/E in the non-adapted eye will be determined exclusively by the diffuse light stimulation of that eye. If not, will there be a 'summation' effect when opponent colours are simultaneously presented in the two eyes, and a 'wiping out' effect when the colours are the same? These would be possibilities if a colour in one eye channel has the same effect in the other channel as the opponent colour (MacKay and MacKay, 1973; 1975).

The results provide firm evidence for interactive effects of the colour features between the eye channels. It can be seen that when the colour is the same in the two eyes, the strength of induced A/E in the non-adapted eye is comparable with results following achromatic pattern stimulation of one eye. The polarity of the A/E is the same in the two eyes, as if the pattern had transferred correctly. There is no evidence for a 'wiping out' as seemed possible if the eye channels are antagonistically cross-coupled with respect to colour.

However, when the colours are opposite in the two eyes, there is clear evidence for a 'wiping-out' effect. The measured A/E is very small or not significant on three out of the four occasions, and is not subjectively visible on any. The polarity of the effect as measured on the three occasions is opposite to that in the adapted eye, as if the pattern information had again transferred correctly and become 'associated' with the colour present in that eye channel. The opponent colours in the two eyes must have interacted in an antagonistic fashion to reduce the A/E strength so sharply compared with the other condition. The results cannot be related in any simple way with the idea that the two monocular colour-signalling channels are antagonistically cross-coupled. For both conditions, the site of interocular interaction is likely to be at a level prior to that at which the pattern and colour are combined.

Two other papers provide evidence for interocular interaction of colour. Sharpe (1974) measured threshold elevation for detecting a red grating and a blue grating following adaptation to one of these. The adapting grating was presented at supra-threshold level, but with the intensity adjusted so as not to excite the channel responsible for detecting the other of the two colours used. When both eyes were adapted, thresholds for detecting the test grating were raised, and elevation was about the same irrespective of the colour of the adapting grating. When only one eye was exposed, the effect transferred, but thresholds were raised substantially more when the test and adapting colours were different. Although Sharpe's general interpretation is open to question, his results do seem to imply some form of antagonistic coupling between the monocular channels. However, since thresholds were also raised when test and adapting colours were the same, some information must be transferred correctly.

Cosgrove et al. (1974), on the other hand, found greater transfer effects when testing and adapting colours were the same. Their technique involved measuring the 'fade' time of a retinally stabilised coloured line presented immediately following adaptation to an unstabilised grating of the same or opponent colour. When test and adapting stimuli were presented to the same eye there was an immediate decrease in the visibility of the line, but only when test and adapting colours were the same. Similar results were found in the dichoptic condition when the test stimulus was presented to the non-adapted eye, but the effect persists for a shorter time. The results would seem to imply that colour information is transferred correctly.

In summary, these experiments provide no evidence to suggest interocular transfer of pattern-contingent chromatic aftereffects. Transfer of pattern information could be accounted for by interaction at a pre-cortical site, as there is only limited evidence for interaction of orientation information. There is clear evidence of interaction of colour information between monocular channels, though the nature of the interocular couplings which could account for the observed effects is not clear. Interocular interaction of both form and colour could occur at a site at which orientation information is not important and prior to the level at which orientation and colour are combined.

APPENDIX C:

THE EFFECT OF VARIOUS DRUGS ON INITIAL STRENGTH AND DECAY SLOPE OF THE MCCOLLOUGH EFFECT

Introduction

The exploratory experiments indicated that for any particular temporal sequence of stimulation, results may vary substantially from one occasion to the next. One possible explanation for the observed variability is in terms of the general level of arousal of the subject. This question had been considered earlier and a log had been kept of sleep habits and day time activity patterns for one subject (KB). However, this had provided no positive clues as to the source of the variability. Moreover, restricting experimental sessions to a particular period of day appeared to do nothing to reduce this variability. The results obtained later as part of the parametric study indicated that some of the variability may be related to the temporal parameters themselves. But the problem of biological variability suggested the possibility of attempting to experimentally manipulate arousal level by the use of appropriate drugs, and to check for systematic changes in strength or decay slope of the A/E. This was discussed with Professor D.M. MacKay, who already had available a number of suitable drugs prescribed by a qualified medical practitioner.

Procedure

Professor D.M. MacKay had complete control of drug administration and K.B. acted as subject in all experiments. The subject had no knowledge of either the classes of drugs to be used or the particular compounds, nor whether placebo trials would be included. To prevent visual recognition of the particular compounds by their shape, size or colour, drugs were always given to the subject while his eyes were shut. Drugs were always administered early to mid morning and 1 to 2 hrs. was allowed before commencing adaptation to allow full absorption of the compound.

Experiments were conducted at randomly spaced intervals over a period of two months, commencing in mid February 1975. In addition to the controls regarding drug administration, the subject also ensured that about 7 hrs. sleep was obtained on the night before experimental sessions (this was a typical duration for the subject), and that breakfast (taken at 8.30 to 9 a.m.) consisted of cereal and one cup of instant coffee. During the experimental session, and for the rest of the day, a record was maintained of activities, general mental state and any 'abnormal' feelings which could possibly be related to the effects of the compound taken.

To facilitate comparison of results, a stimulation sequence of 10 sec. ON/1 sec. OFF was used on all occasions. The exploratory experiments had indicated that initial strengths and decay slopes were fairly consistent for repeat runs using this sequence. The subject was exposed for 10 min. to the usual McCollough patterns.*

Results and Discussion

The results are shown in Fig. C.1, and are summarised in Table C.1. It can be seen that initial strengths are not significantly reduced, compared with results for the control condition having a 10 min. adaptation duration

---

*(Footnote) N.B. Since a tachistoscope was in use by this time, and the post-adaptation conditions controlled, an exposure duration of 15 min. would have been more appropriate. For this reason, two control conditions are shown, one being averaged data points for the first 40 min. of decay and are the results of the exploratory experiments using this stimulation sequence. The other is taken from the results presented in Chapter 4.

FIG C1

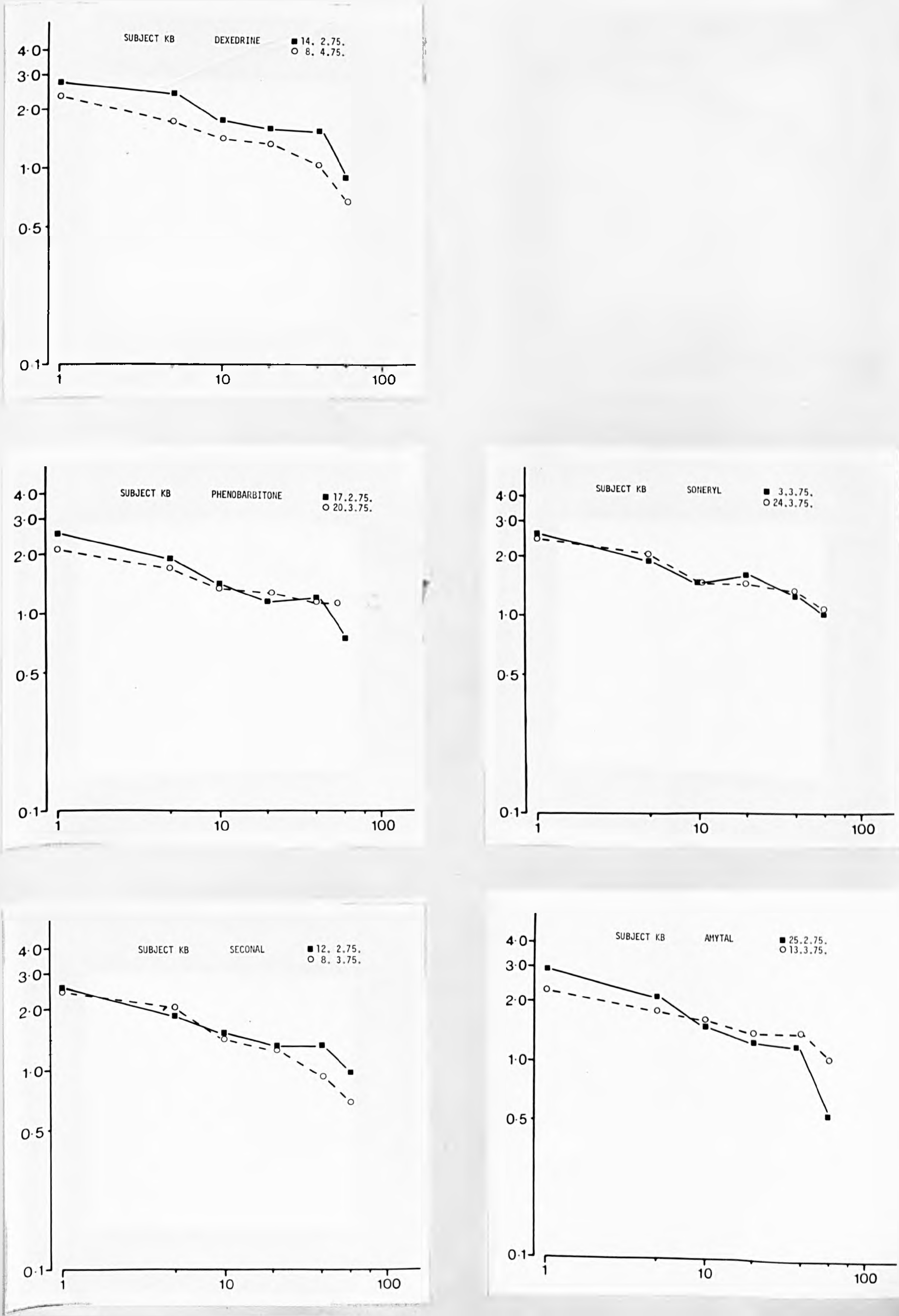
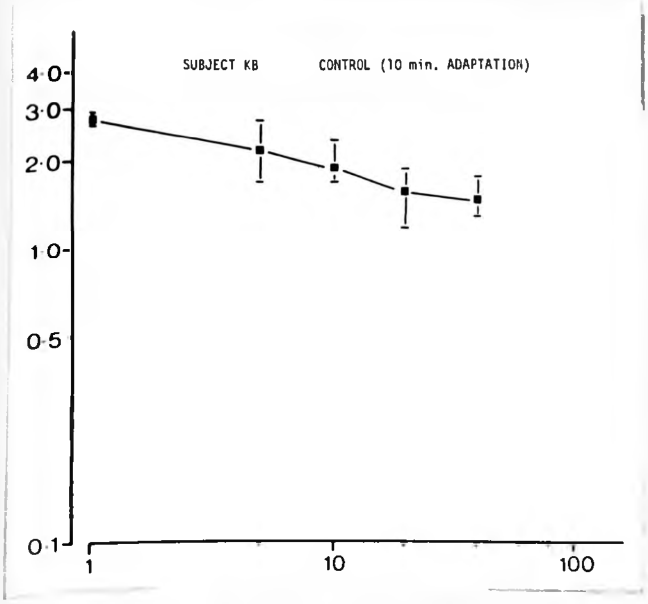

SUBJECT KB
DEXEDRINE
■ 14. 2.75.
○ 8. 4.75.
4·0
3·0
2·0
1·0
0·5
0·1
1
10
100
SUBJECT KB
PHENOBARBITONE
■ 17.2.75.
○ 20.3.75.
SUBJECT KB
SONERYL
■ 3.3.75.
○ 24.3.75.
SUBJECT KB
SECONAL
■ 12. 2.75.
○ 8. 3.75.
SUBJECT KB
AMYTAL
■ 25.2.75.
○ 13.3.75.

FIG C1


SUBJECT KB
CONTROL (10 min. ADAPTATION)
4·0
3·0
2·0
1·0
0·5
0·1
1
10
100

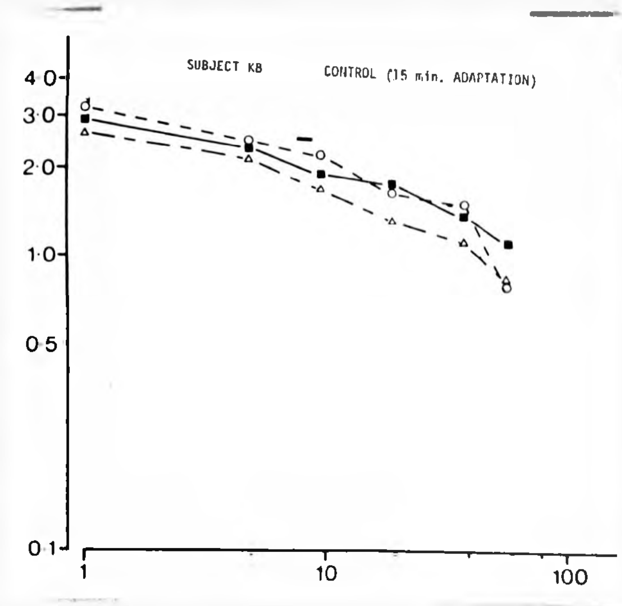

SUBJECT KB
CONTROL (15 min. ADAPTATION)
4·0
3·0
2·0
1·0
0·5
0·1
1
10
100

TABLE C.1 EFFECT OF VARIOUS DRUGS ON INITIAL STRENGTH AND DECAY SLOPE OF THE MCCOLLOUGH EFFECT

Drug and Classification	Normal Dosage (mgs.)	Date and time commenced adapt.	Drug Dosage (mgs.)	Initial Strength		Decay Slope		Subjective Effects/ Comments
				Values	Mean	Values	Mean	
Dexedrine (Amphetamine).	10	14. 2.75 12.15 pm 8. 4.75 10.45 am	5 5	2.8 2.3	2.6	-0.24 -0.28	-0.26	None None
Second (Barbiturate)	100-200	12. 2.75 11.25 am 8. 3.75 11.35 am	100 100	2.5 2.5	2.5	-0.21 -0.31	-0.26	Felt drowsy Felt drowsy
Phenobarbitone (Barbiturate)	60-200	17. 2.75 11.55 am 20. 3.75 11.00 am	30 30	2.5 2.1	2.3	-0.28 -0.16	-0.22	None None
Amytal (Barbiturate)	100-200	25. 2.75 11.20 am 13.3.75 10.55 am	30 30	2.9 2.3	2.6	-0.35 -0.17	-0.26	None Felt drowsy
Soneryl (Barbiturate)	100-200	3. 3.75 12.50 am 24. 3.75 11.00 am	100 100	2.6 2.6	2.6	-0.21 -0.21	-0.21	None Felt drowsy
Control (No drugs given) 10 min. Adapt. Free post-adaptation environment		6. 2.74 11.05 am 29. 3.74 12.45 pm 7. 6.74 10.15 am 23. 6.74 11.30 am 12.10.74 10.45 am		2.8 2.9 2.7 2.9 2.7	2.7	-0.23 -0.29 -0.36 -0.21 -0.20	-0.26	
Control (No drugs given) 15 min. Adapt. Controlled post-adapt. illumination		5. 3.75 9.45 am 6. 3.75 9.40 am 7. 3.75 9.40 am		3.4 2.8 3.3	3.1	-0.29 -0.27 -0.22	-0.26	

(it should be remembered that these adaptation procedures were not identical with those of the other experimental conditions). Neither amphetamines nor barbiturates therefore had any measurable effect on the process of establishment of the A/E in these experiments. Decay slopes following administration of the amphetamine are within the normal range, as are those for one of the barbiturate group. Decay slopes associated with administration of the other barbiturates varied substantially between repeat experiments, but the direction of the observed changes were not consistent. For each of the three drugs, the associated decay slopes were at the two extremes of the normal range. Mean values did not vary significantly.

It would appear that drugs which would be expected to influence the general level of arousal do not have any specific effect on the mechanism underlying establishment and decay of the McCollough Effect. The differences observed are perhaps better attributed to a more general effect of the drugs on the central nervous system. Recently, Shute (1978) has presented results suggesting that drugs having a hyperpolarising effect on central neurones give rise to a decreased rate of decay. He administered drugs orally immediately after the first test following adaptation, and found that strength values were raised and decay rate decreased by acetylcholine blocking agents (hyoscine, ethopropazine and mecamylamine). He concluded that these results support the hypothesis that the strength of the A/E reflects the level of central inhibition of the adapting colour. Rather surprisingly, in view of the results presented here, he also found that strength values were lowered and decay rate increased by caffein, which he attributed to be depolarizing, acetylecholine - like effect. In this study, Dexedrine had no significant effect on the A/E, but administered doses were below the normal for this compound, and it would be difficult to compare different compounds and dosage.

APPENDIX D: HYSTERESIS

To allow sufficient data to be collected for the experiments described in Chapters 4 and 5, one subject (KB) was exposed to the McCollough patterns for 15 min. on most days of the week (including weekends), during the whole of the second year of the project. Decay was plotted under conditions of controlled illumination for 1 hr. following the end of adaptation. At the end of this period, the A/E was neutralised by a few minutes exposure to the opposite pairing of colour and grating orientation, and a visual inspection of the test card ensured that there was no more than a small residual A/E. On the following day, at about the same time, the subject adapted to this pairing of colour and pattern, and so on. The initial reading on most occasions confirmed that there was no more than a small orientationally linked colour bias. Such frequent experimental sessions involving a long-lasting A/E obviously carried considerable dangers that establishment of the A/E could be impeded by a residual effect from the preceding experimental session; or that the normal rate of decay could be modified because of the frequent changes being induced in the mechanism underlying the effect.

To check on this possibility, the following test was carried out at the commencement of the projects described in Chapter 4 and 5. Experimental sessions were carried out as already described, but the same temporal sequence of stimulation was used on each day over a three week period, and the results are summarised in Table D.1. During the first week the subject (KB) was exposed for 20 min., but this induced A/E's whose initial strength tended to be beyond the range of the measuring apparatus. Calculated decay slopes therefore tend to be on the steep side, for reasons already discussed in Chapter 7. However, it can be seen that there is no systematic

TABLE D.1 TEMPORAL SEQUENCE: 1 SEC. ON/1 SEC. OFF

DATE	INITIAL BIAS	20 MIN. ADAPTATION		15 MIN. ADAPTATION	
		INITIAL STRENGTH	DECAY SLOPE	INITIAL STRENGTH	DECAY SLOPE
1.11.74	NIL	3.5	-0.32		
2.11.74		NO EXPERIMENT		NO EXPERIMENT	
3.11.74	NIL	N.M.	-0.42		
4.11.74	NIL			2.7	-0.42
5.11.74	NIL	N.M.	-0.48		
6.11.74	NIL	4.7	-0.47		
7.11.74	NIL	N.M.	-0.48		
8.11.74	NIL			3.1	-0.35
9.11.74		NO EXPERIMENT		NO EXPERIMENT	
10.11.74		NO EXPERIMENT		NO EXPERIMENT	
11.11.74		NO EXPERIMENT		NO EXPERIMENT	
12.11.74		NO EXPERIMENT		NO EXPERIMENT	
13.11.74		NO EXPERIMENT		NO EXPERIMENT	
14.11.74	L=+0.4/R=-0.2			3.1	-0.31
15.11.74	L= 0.3/R=NIL			2.7	-0.31
16.11.74		NO EXPERIMENT		NO EXPERIMENT	
17.11.74	L=+0.3/R=+0.2			2.4	-0.28
18.11.74	NIL			2.9	-0.32
19.11.74	NIL			2.6	-0.37
20.11.74	NIL			2.7	-0.46

NIL: INITIAL BIAS $\leqslant$ 0.1

+ : INITIAL BIAS OPPOSITE POLARITY TO SUBSEQUENTLY INDUCED A/E

- : INITIAL BIAS SAME POLARITY AS SUBSEQUENTLY INDUCED A/E

TABLE D.1 (contd.) TEMPORAL SEQUENCE: 10 SEC. ON/1 SEC. OFF

DATE	INITIAL BIAS	20 MIN. ADAPTATION		15 MIN. ADAPTATION	
		INITIAL STRENGTH	DECAY SLOPE	INITIAL STRENGTH	DECAY SLOPE
5.3.75	NIL			3.4	-0.29
6.3.75	NIL			2.8	-0.27
7.3.75	NIL			3.3	-0.22

NIL: INITIAL BIAS $\leq$ 0.1

+ : INITIAL BIAS OPPOSITE POLARITY TO SUBSEQUENTLY INDUCED A/E

- : INITIAL BIAS SAME POLARITY AS SUBSEQUENTLY INDUCED A/E change in calculated slope over the eight days in question. There was then a four day break, but when experimentation was resumed, this time with only a 15 min. adaptation duration, initial strength and decay slope were very similar to the previous result. Results were similar on the next day, which was followed by a one day break. Over the succeeding four days there was no systematic change in initial strength, but decay slope became progressively steeper. This was contrary to the findings of the first week. Four months later, a 10 sec. ON/1 sec. OFF sequence was used on three successive days, and on this occasion decay slope became progressively less steep.

These experiments therefore failed to provide clear evidence of systematic changes in either initial strength or decay slope resulting from repeated exposure under the conditions described.

APPENDIX E:

RECENT FINDINGS RAISING DIFFICULTIES FOR THEORY OF THE MCCOLLOUGH EFFECT

Chapter 1 reviewed much of the basic literature on the McCollough Effect. The findings summarised there are consistent with McCollough's original idea that single units tuned to both orientation and wavelength may be fatigued by prolonged stimulation. A number of recently published findings are thought to present a challenge for this form of explanation. For convenience, these findings may be reviewed under two headings. Firstly, those relevant to the 'double-duty edge-detector' aspect of the hypothesis and, secondly, those relevant to the 'fatigue' theory.

E.1 Experimental findings which complicate the picture for the 'double-duty edge-detector' apsect of the theory

E.1.1 Multiple contingent A/E's

It has been shown that contingent A/EPs can be established for a number of stimulus dimensions other than orientation and colour. Hepler (1968) has shown that following 27 min. exposure to a red grating moving downwards alternating with a green grating moving upwards, the apparent colour of an achromatic grating is dependent on its direction of motion. All subjects reported a negative colour A/E specific to the two directions of motion used in adaptation, the effect persisting for 20 hrs. or longer. This may be termed a colour A/E contingent on direction of motion.

Mayhew and Anstis (1972) reported that motion A/E lasting several days can be made contingent on a number of dimensions. In the first experiment S adapted for 10 min. to a spiral-patterned disc rotating clockwise under red light and counterclockwise under green light. When stopped, the disc then appeared to rotate counterclockwise under red and clockwise under green light. The effect lasted only a second or two, reappearing each time the field's colour was changed, and there was a build-up in strength in the first half hour of testing. Colours similar in wavelength to the adapting colours could also elicit the A/E, under yellow light the pattern appearing to rotate counterclockwise and clockwise under blue light. Similar motion A/E were produced by pairing direction of movement with intensity, with width of moving stripes and with orientation of a stationary grating projected onto a rotating patterned disc.

Colour-contingent A/E have also been found for other forms of pattern. Hajos (1967) briefly reported that A/E could be built up to patterns that "... comply with the receptive fields of the colour detectors in the lateral geniculate nucleus". Leppmann (1973) has also reported that chromatic A/E can be produced with stimulus attributes totally independent of orientation. A/E were established which were specific to the spatial frequency of grating patterns in one experiment, and to concentric circles in another experiment. The strength of effect decreased as the space frequency of the test pattern was varied relative to that of the adapting patterns. Leppmann suggested that units must exist which were specific to both space-frequency and colour.

A/E have also been established to patterns made up of regularly arranged dots (MacKay & MacKay, 1975). Subjects viewed, say, large red dots alternating with small green dots for 10 or 20 min., subsequently all subjects reporting complementary hues on black-and-white test patterns of the corresponding angular subtense. Negative test patterns gave similar but weaker effects. The strength of the A/E is weaker than that of the normal McCollough Effect. Aperiodic stimuli such as randomly arranged dot patterns and 'visual noise' patterns differing in scale also give clear though much weaker effects. MacKay and MacKay (1975) argued that their results indicate that neither uniquely oriented nor spatially periodic stimuli are essential and that texture-density differences alone can be sufficient to elicit chromatic A/E.

MacKay and MacKay (1975) also argued that if independent neural channels respond to line-orientations and local texture density, it should be possible for chromatic A/E of each kind to co-exist without interference. In a further experiment, subjects were exposed for 5-10 min. to alternating red left-oblique and green right-oblique gratings, and then for a further 5-10 min. to alternating dot patterns. Both A/E were clearly present. Either could be elicited, for an hour and more after adaptation, by presenting black-and-white versions of the original stimulus-pairs. Wyatt (1974) has reported that colour A/E can be made contingent on two dimensions (frequency and orientation) simultaneously.

None of these results in themselves rule out the hypothesis that the neural units that undergo chromatic adaptation are individually orientation specific. Leppmann's stimuli approximate to periodic rectilinear gratings if one considers only restricted parts of the visual field; and it is already known that different retinal regions can develop independent associations of hue and colour (Harris, 1969; Stromeyer, 1969). The results related to moving bars, and to grating patterns of various space frequency also imply involvement of orientationally tuned units. The results of the MacKays indicate that neither uniquely oriented nor spatially periodic stimuli are essential, without implying anything about the mechanisms signalling texture density. What they do imply is that different stimulus pattern features need not be processed by different cortical detectors (i.e. we need not think of a special detector for every possible feature).

The greater importance of these findings revolves around their implications for estimates of the number of detectors conjointly tuned to two or more dimensions, rather than the sorts of pattern features which can elicit an A/E. Thelist of ordinary and contingent A/E must now imply detectors specific for orientation, space frequency and movement alone and to each of these conjointly tuned for a specific colour. The theory might even require units specific to three or even all of these dimensions. So even if one takes a restricted interpretation of some results, they do imply a growing number of categories of units which are presumed to exist in the visual cortex. This indeed may be the case, but the greater the number, the less appealing does this form of explanation become.

E.1.2 Anomalous findings regarding interocular transfer and the McCollough Effect

Of further interest are a number of anomalous findings regarding interocular transfer of the A/E. If units exist which are conjointly tuned to two stimulus dimensions, then in an interocular transfer situation the A/E to both dimensions should transfer or neither should transfer, but not one alone. Murch (1972) used a variation of the size effect (Blakemore & Sutton, 1969). One half of the adapting pattern consisted of a grating pattern with wide stripes and the other half of a grating pattern with narrow stripes. The subject fixated a marker between the two. The whole pattern was viewed through red light in one orientation and green light in the orthogonal orientation. The test card was structured in the same way but stripe widths were the same in the two halves. After monocularly viewing the alternation of the two orientations, 80% of subjects report the size A/E in both the adapted and non-adapted eyes. However, only 50% of subjects report the colour A/E even when the test patterns were presented to the adapted eye, and only 4% gave a colour report for the non-adapted eye.

Similar findings have been reported for the tilt A/E. Broerse, Over and Lovegrove (1975) found that the tilt A/E transfers but with a loss of the wavelength selectivity characteristic of the A/E in the adapted eye. These results would tend to imply that a single mechanism does not mediate both the spatial and chromatic components of these A/E's.

E.1.3 Effects of pre- and post-adaptation illumination conditions

A further difficulty for the "double-duty" hypothesis is that diffuse colour or achromatic patterns presented alone can have a significant influence on the characteristics of the A/E or on its subsequent rate of decay. Hirsch and Murch (1972) argued that if the coloured pattern was processed at the cortical level by a single population of units, the resulting A/E should not be influenced by a post-adaptation exposure to diffuse (patternless) colour. In the control condition, subjects had a normal McCollough effect induced. On a subsequent occasion, the adaptation was preceded by a period of exposure to alternating coloured fields (yellow and blue) whose wavelengths closely bracketed those of the McCollough patterns. Post-adaptation colour matches indicated that the colours of the A/E had shifted away from the colours of the post-adapting fields and towards the portions of the spectrum not adapted out by the preceding plain colours.¶ Skowbo, et al. (1975) have shown that post adaptation exposure conditions may affect the rate of decay of the A/E. Normal McCollough A/E were built-up by 10 min. exposure to alternating coloured gratings. Each adaptation period was followed by 50 min. of exposure to one of the following conditions: (1) alternating achromatic gratings with the same orientations as those of the adapting patterns, (2) alternating homogeneous coloured fields, colours being identical with those of the test pattern, (3) normal visual environment, (4) complete darkness, (5) alternating chromatic gratings with colour/orientation pairings reversed relative to adaptation. The results for conditions (2), (3) and (4) were indistinguishable from each other. Condition (5) resulted in a cancellation of the A/E and then a build-up of an A/E of opposite polarity, but this was expected on the basis of previous reports (Hajos, 1968; Stromeyer, 1969). More surprisingly, exposure to achromatic gratings was associated with a more rapid decay of the A/E. This finding has been confirmed (see MacKay and MacKay, 1975). It is not known whether pre-exposure to achromatic gratings would have the same effect.

More recently, Murch (1976) has shown that a short period of exposure to achromatic gratings or diffuse colour during the adaptation sequence can have a critical influence on the strength of induced A/E. Subjects were exposed to normal McCollough patterns alternating every few seconds. Onset of either the pattern or the colour elements of the stimuli could be delayed relative to the other, with simultaneous offset. The strongest A/E were found when there was no delay, or when the colour was delayed by only half a second. Very weak A/E were observed if the colour was delayed by 1 sec. relative to pattern onset, or if the pattern was delayed by only ½ sec. That is, ½ sec. or 1 sec. of exposure to the colour or the achromatic grating elements alone immediately prior to pattern and colour stimulation was sufficient to prevent normal build-up of the A/E. If the "double-duty" theory were correct, one would assume that the colour and achromatic pattern would be processed by separate subpopulations and would not excite units tuned to pattern <u>and</u> colour.

E.2 Evidence presenting difficulties for the "fatigue" theory

E.2.1 Lack of spontaneous decay in darkness

The hypothesis that the mechanism of adaptation is a fatigue of single units also carries with it the assumption that recovery is itself spontaneous, with a rate determined by some endogenous physiological process. This has turned out not to be the case. Although Skowbo et al (1975) reported that decay during a period of darkness was indistinguishable from that associated with a normal visual environment, MacKay and MacKay (1974 (a) (b); 1975 (a) (b); 1977) have presented convincing contradictory evidence. They noticed that the measured strength of a decaying A/E tended to be slightly higher after a night's sleep. This raised the question whether sleep may refresh the "read-out" mechanism, or arrested the process of decay. Experiments in which an A/E was induced last thing at night showed that practically no decay had occurred when a measurement was taken immediately on waking.

To confirm that darkness per se was the crucial factor, an A/E was binocularly induced early in the morning and a reading taken immediately after exposure. One eye then had all light totally excluded while the other eye received normal stimulation. After 2 hrs. of normal activity the occluded eye was uncovered and both eyes tested. The uncovered eye showed a normal large decay of the A/E, but the strength in the other eye was undiminished. The experiment was repeated, but on this occasion one eye was covered with a patch of thin translucent paper. Testing after several hours of normal activity, strength was found to have decayed by equal and normal amounts in both eyes. Darkness is therefore sufficient to arrest decay totally, but unpatterned light causes the same order of magnitude of decay as patterned light.

To confirm that rate of decay is not affected by this period of occlusion, the MacKays made the following experiment. One eye only was adapted in the normal way, and immediately after adaptation had all light totally excluded by means of an eye-patch. 24 hrs. later and with the patch still on this eye, the other eye was adapted in the same way. The eye-patch was then removed and both eyes tested over a period of several hours. The initial strength and time course of decay in the two eyes were very similar.

These facts point conclusively to arrest of decay when light is occluded, though there may additionally be a transient boost of read-out. If neural fatigue were responsible, there would seem to be no good reason why sleep or darkness should arrest rather than facilitate the recovery process. The results indicate that the main factor normally active in restoring equilibrium after pattern-contingent chromatic adaptation is not an endogenous process, but one dependent on retinal stimulation, which seems equally effective whether patterned or unpatterned. Spigel (1960) has reported that a short period of darkness, following motion adaptation, also increases by a few seconds the persistence of the motion A/E.

E.2.2 Lack of decay when subject not exposed to test card after adaptation?

One other finding is more controversial. Holding and Jones (1976) have reported that decay of the A/E is not initiated until the subject is first exposed to the achromatic test patterns. 90 subjects were randomly assigned to one of three groups. All subjects had a normal McCollough effect induced, but the first testing for one group was 4 hrs. after the end of exposure, 24 hrs. later for the second group and 96 hrs. for the third. A fourth group in a previous experiment had been tested immediately after exposure to the adapting patterns, and were used as a control. There was very little difference in the initial strength between the groups, though it was slightly lower for the two longer delays. Thereafter, decay was normal and very similar for all four groups. Holding and Jones concluded that during the delay interval very little decay occurs, but a single test session is sufficient to initiate the decay process, which is equally protracted whatever the initial delay.

There are a number of problems with the Holding and Jones experiment. Firstly, the values for initial strength are means for a group of 30 subjects. It is well known (e.g. MacKay and MacKay 1973b; Riggs et al., 1974) that similar conditions and durations of adaptation yield very different initial strength across subjects, so pooling data in this way is likely to mask differences between conditions. No indication is given of the scatter around the mean values. Secondly, the points on the decay curve are for three separate sub-groups of ten. Each group of 30 was split into subgroups of 10, who were tested for a second and last time at 4, 24 or 96 hrs. after the first reading. (However, Shute (1977a)) has also reported that very little if any decay occurs if the first testing is delayed by several hours.)

Contrary to these findings, White (1976, p27-29) tested the same subject for a number of delay periods. Comparing results with those for a normal period of testing which commenced at the end of exposure, he found that the A/E does decay. The strength at each delay period corresponded to the measurement from the normal decay taken at an equivalent time period after the end of exposure. Furthermore, he could find no evidence for any effect due to the frequency of testing. V. MacKay (personal communication) has unpublished results which support White. The Holding and Jones (1976) report should therefore be treated with caution.

APPENDIX F: RESULTS OF EXPLORATORY EXPERIMENTS

FIG. I COMPARISON OF TWO TEMPORAL SEQUENCES OF STIMULATION

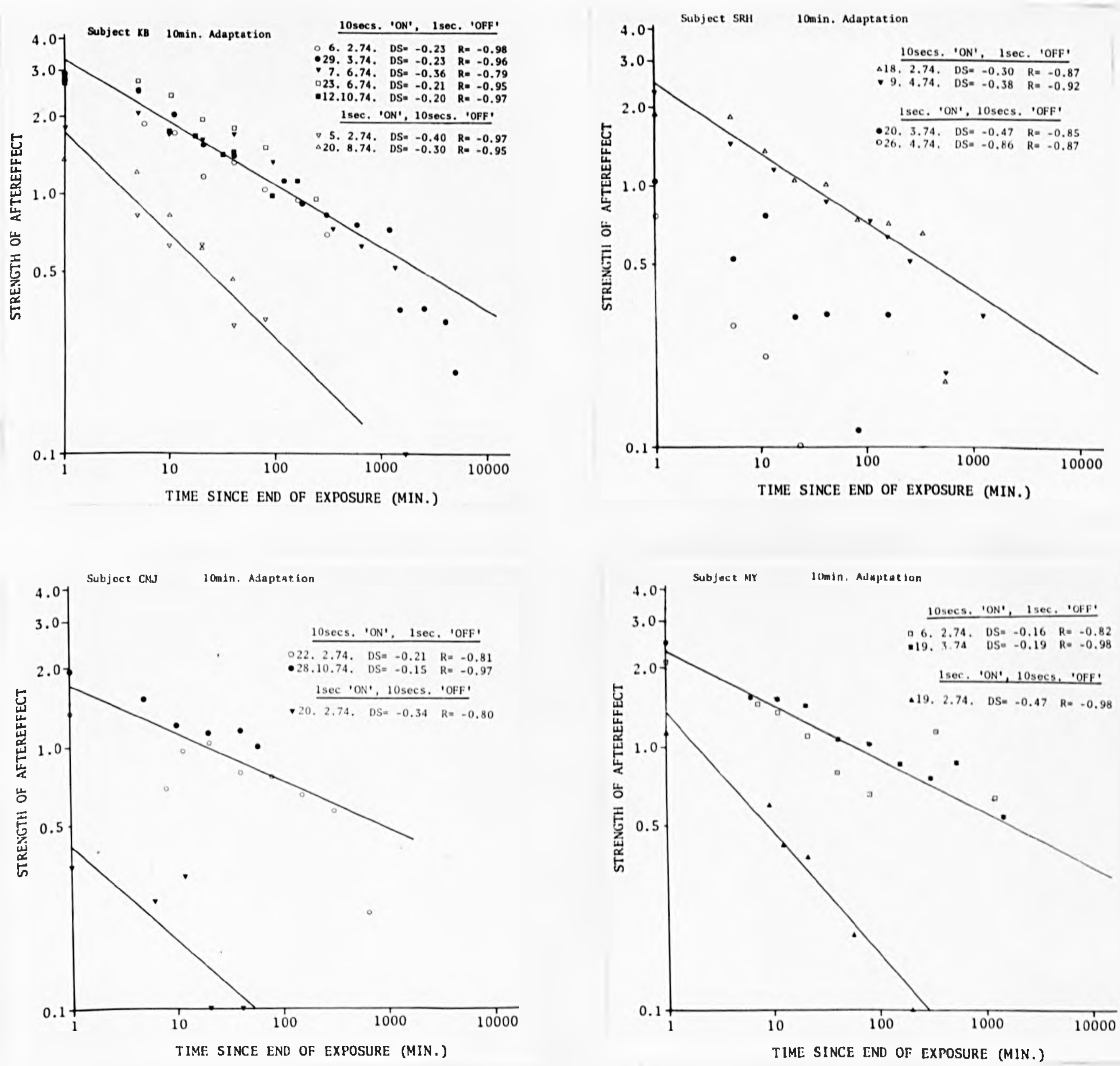


FIG. II TEMPORAL SEQUENCE: 1 SEC. ON/10 SEC. OFF

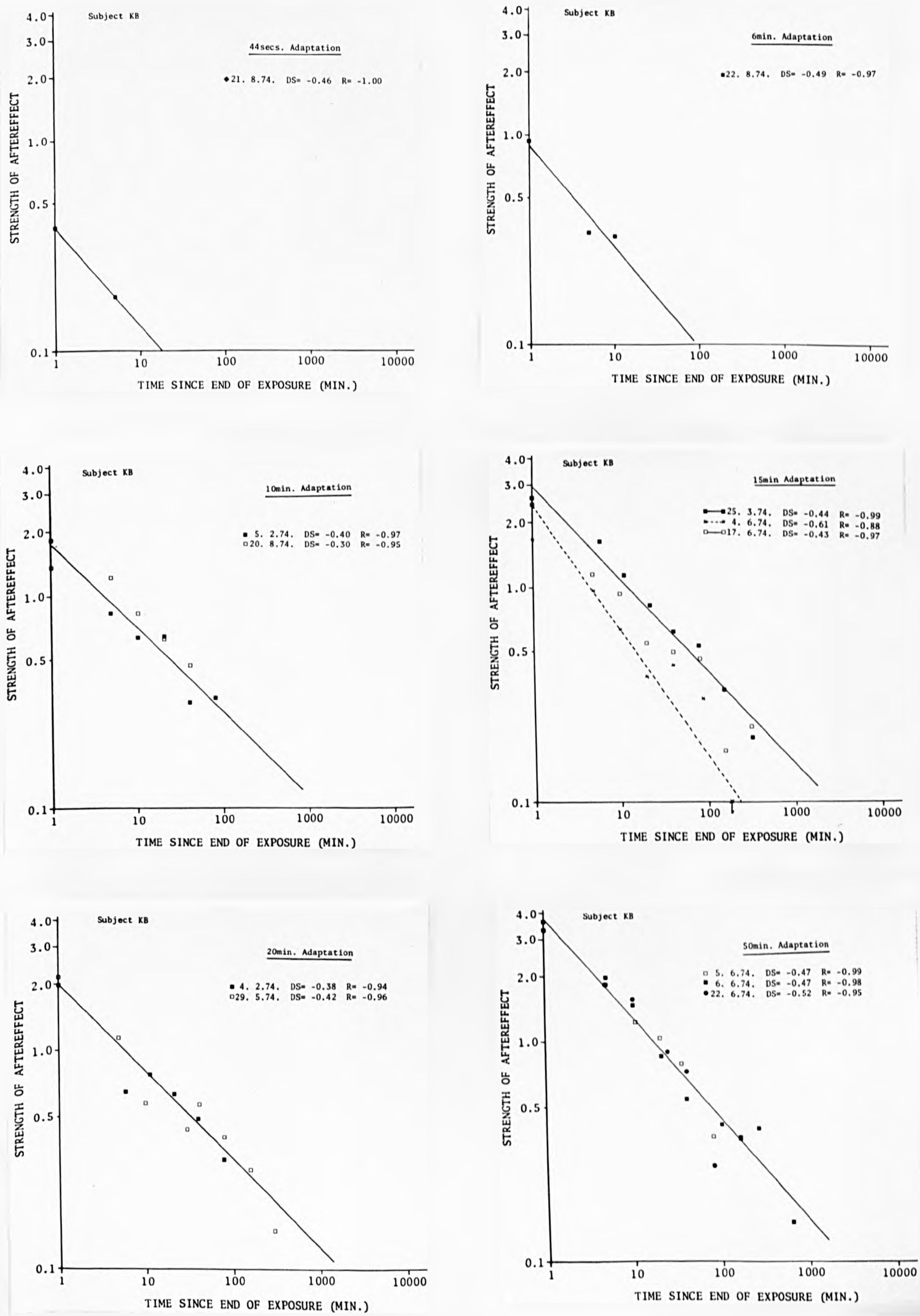
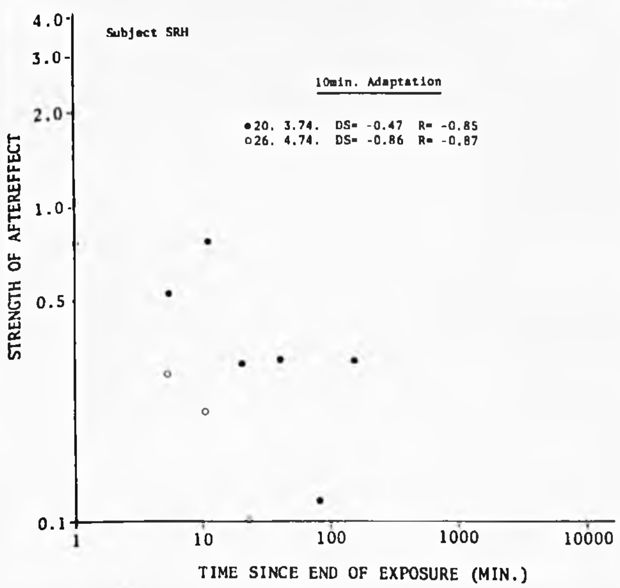
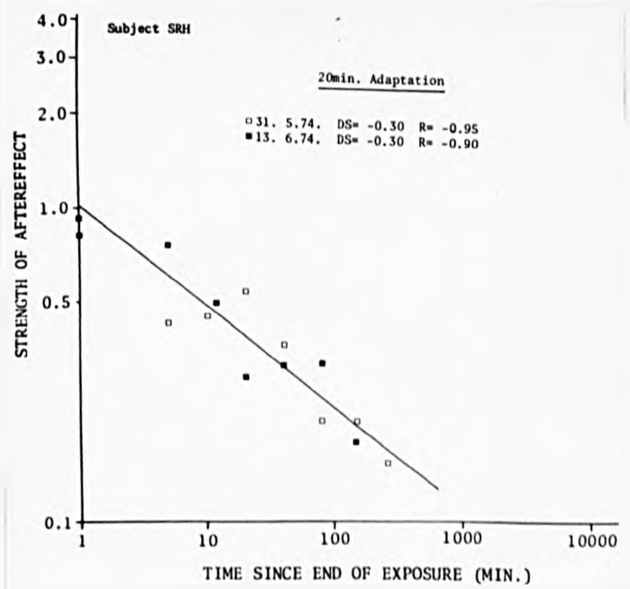
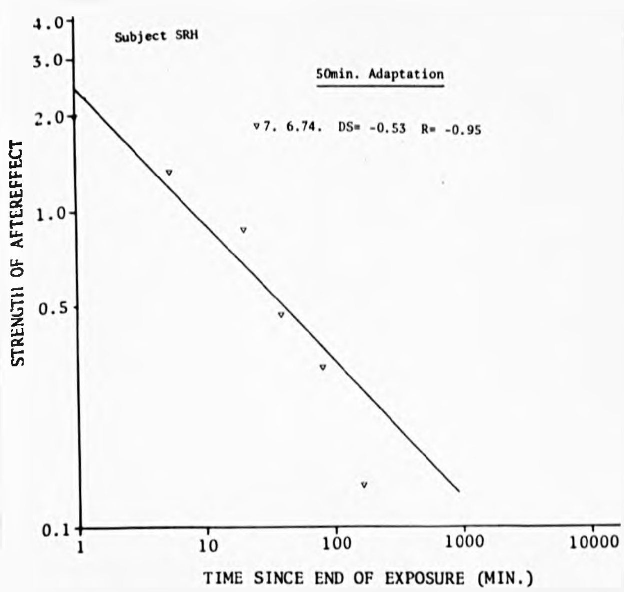
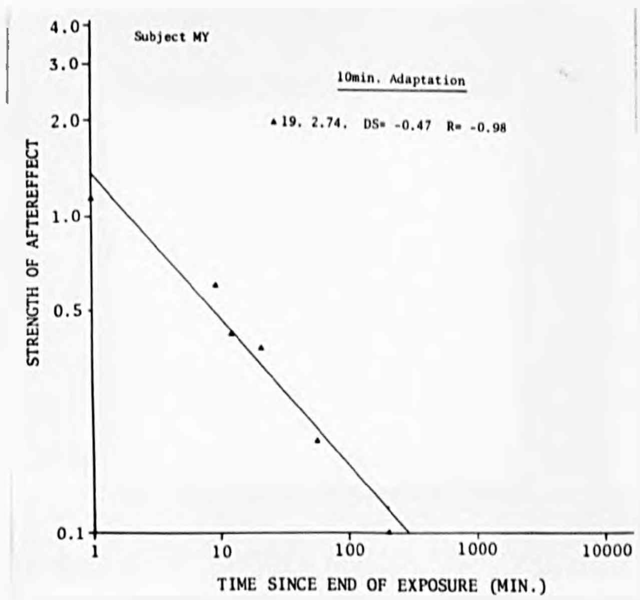


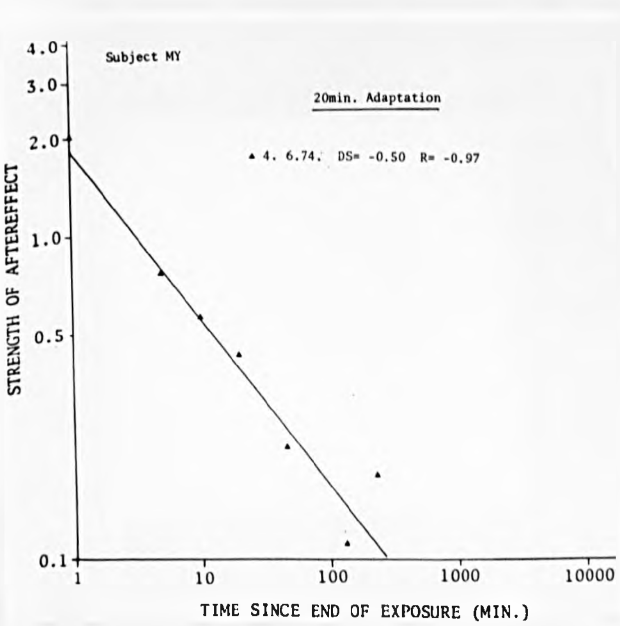
FIG. III TEMPORAL SEQUENCE: 1 SEC. ON/10 SEC. OFF











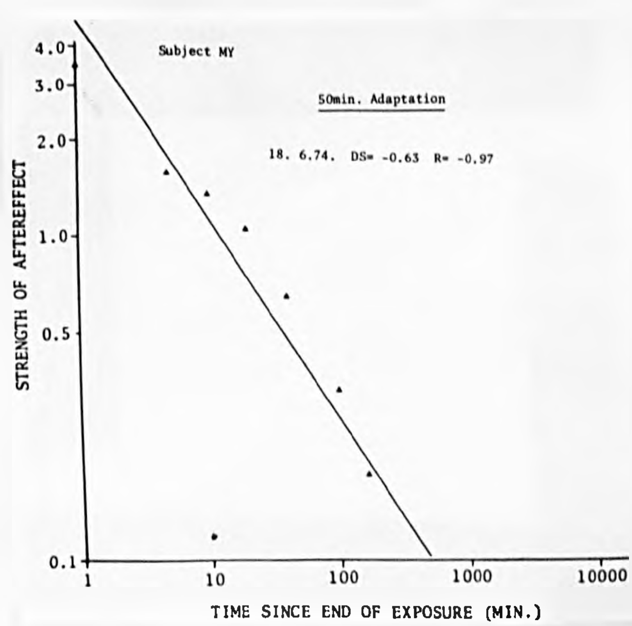


FIG. IV TEMPORAL SEQUENCE: 10 SEC. ON/1 SEC. OFF

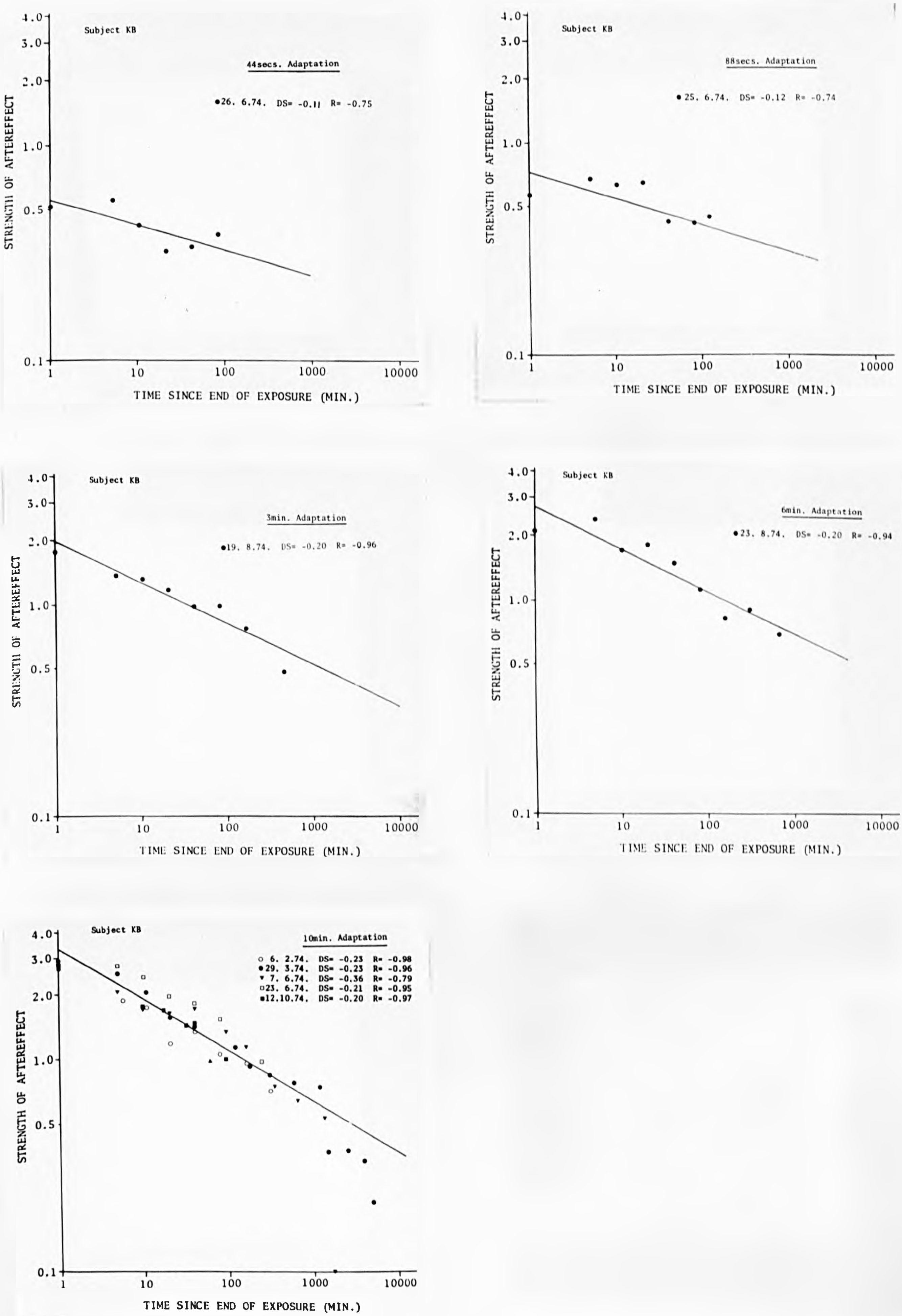


FIG. V COMPARISON OF TWO TEMPORAL SEQUENCES OF STIMULATION

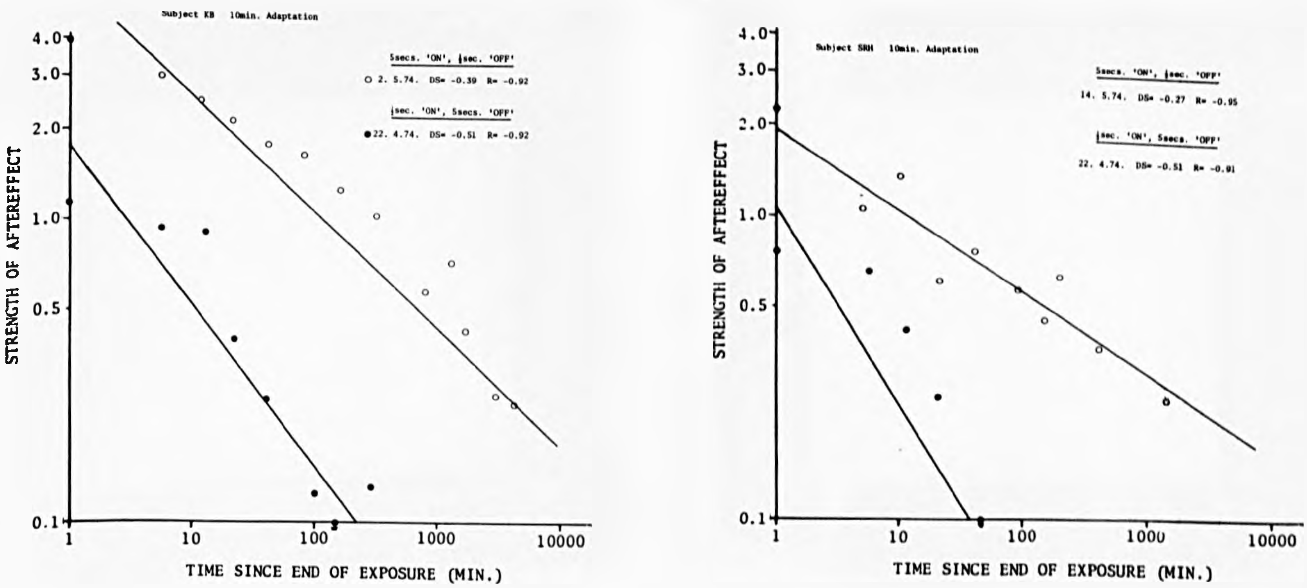
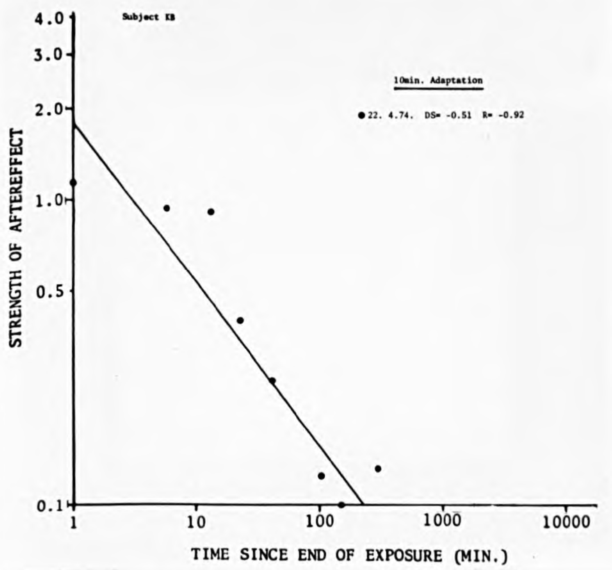
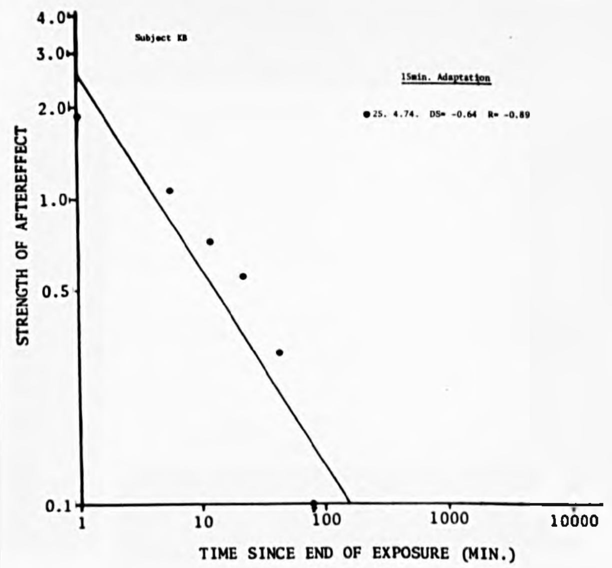
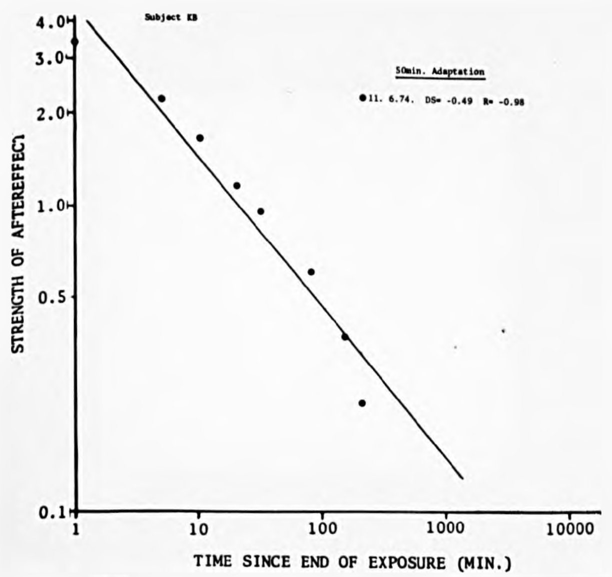
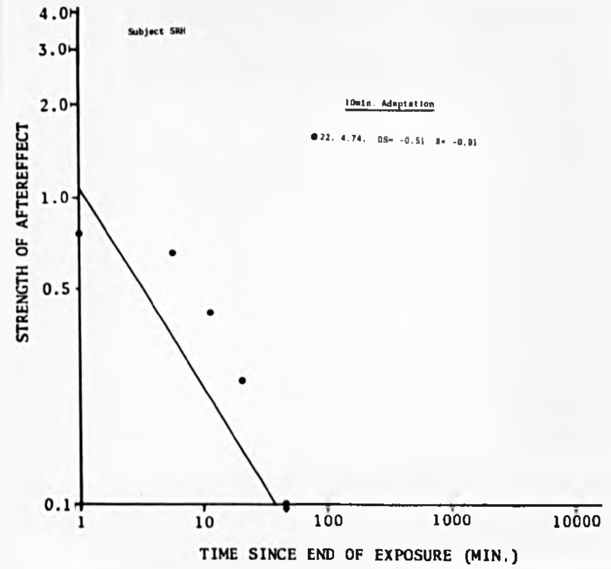


FIG. VI TEMPORAL SEQUENCE: ½ SEC. ON/5 SEC. OFF









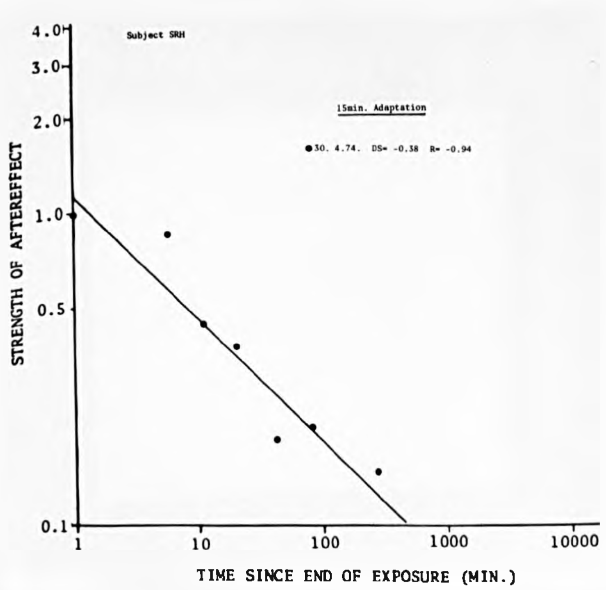
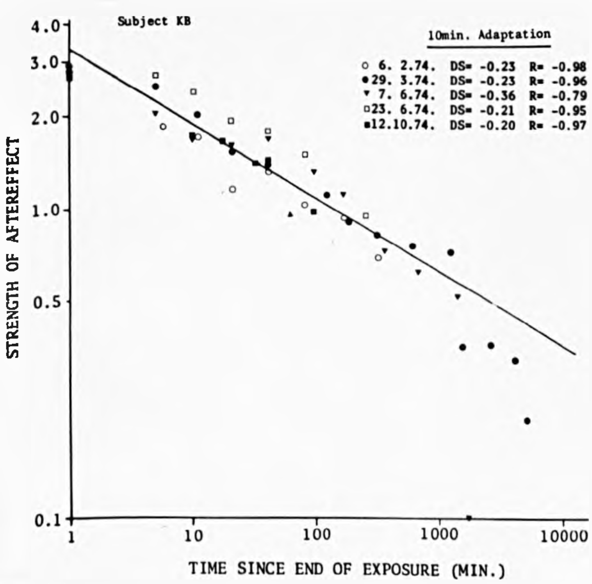
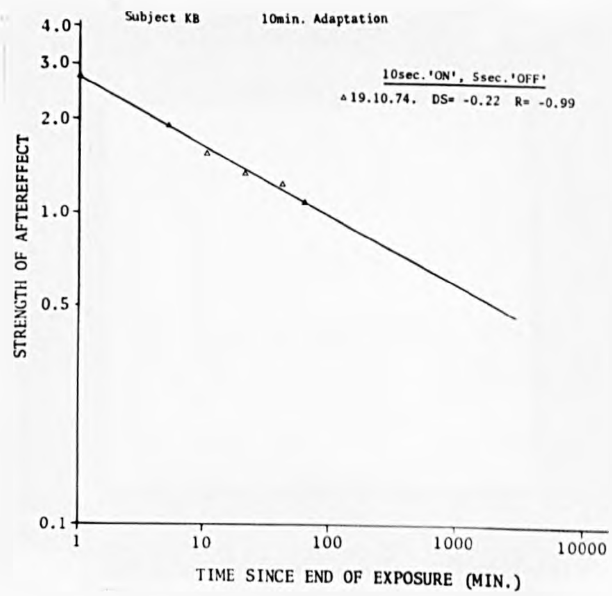


FIG. VII EXPERIMENTS WITH A 10 SEC. 'ON' PERIOD





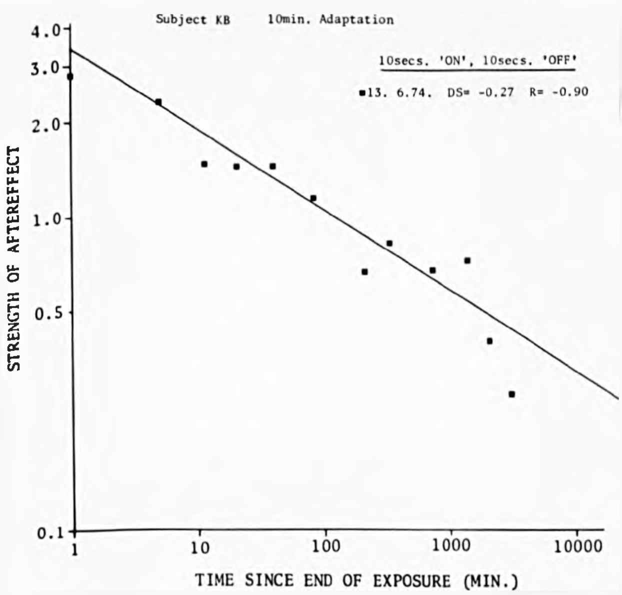


FIG. VIII EXPERIMENTS WITH A 10 SEC. 'OFF' PERIOD

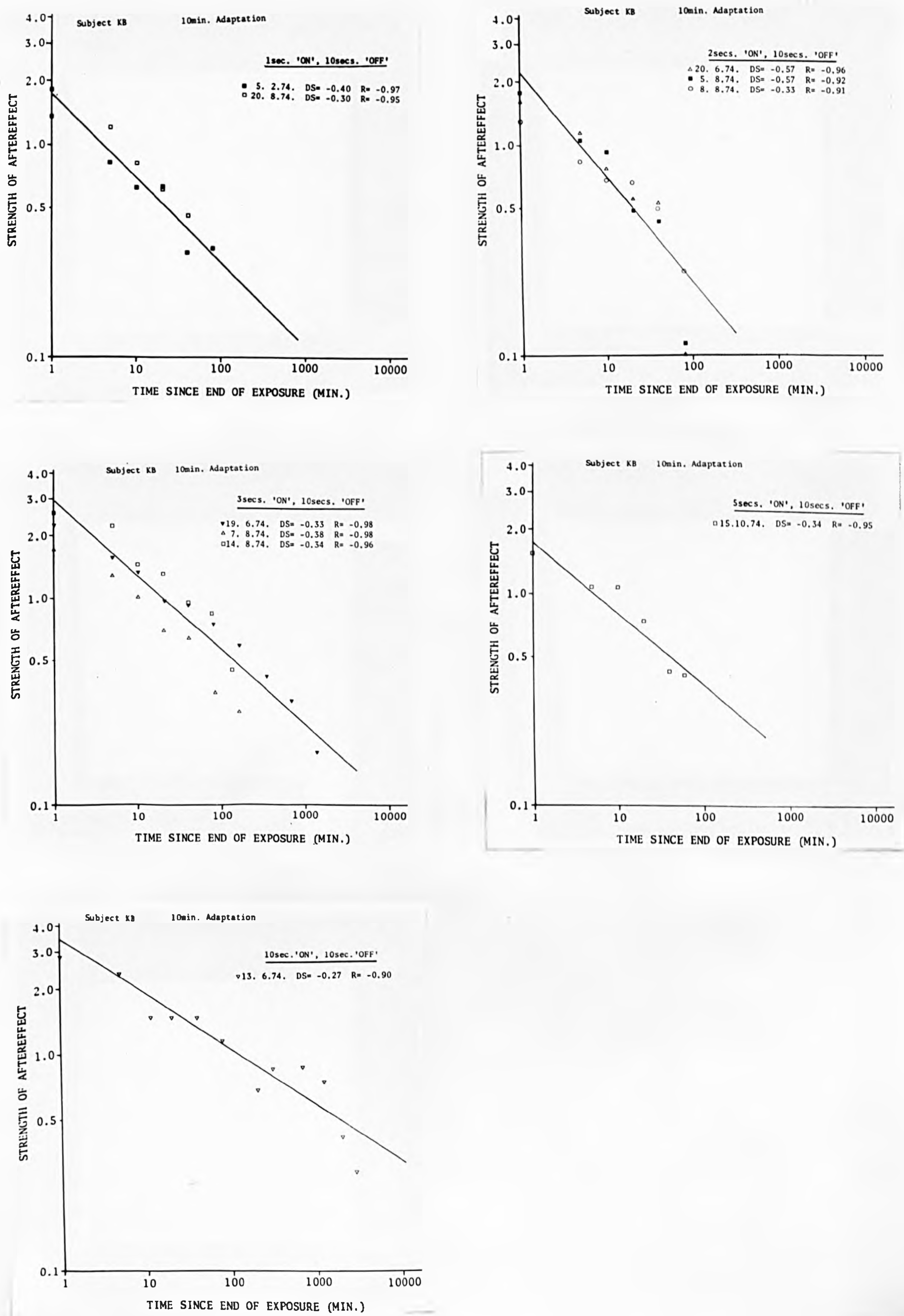
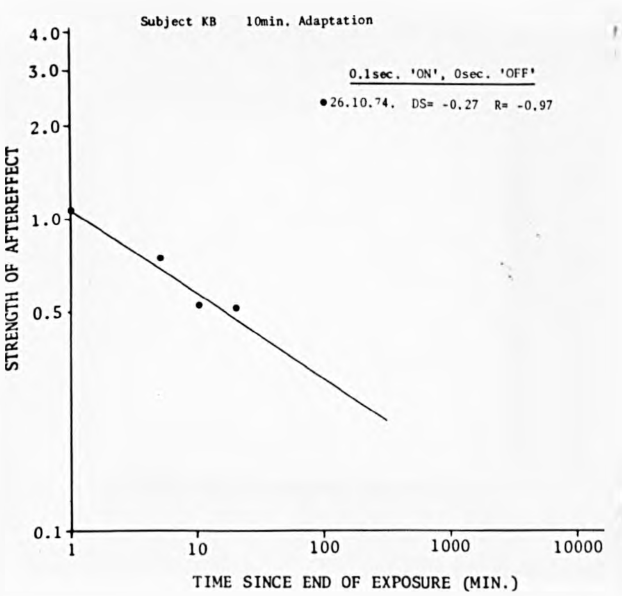
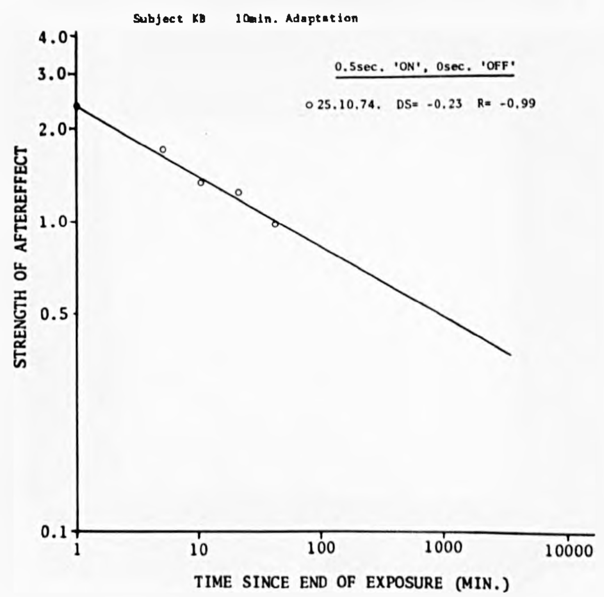
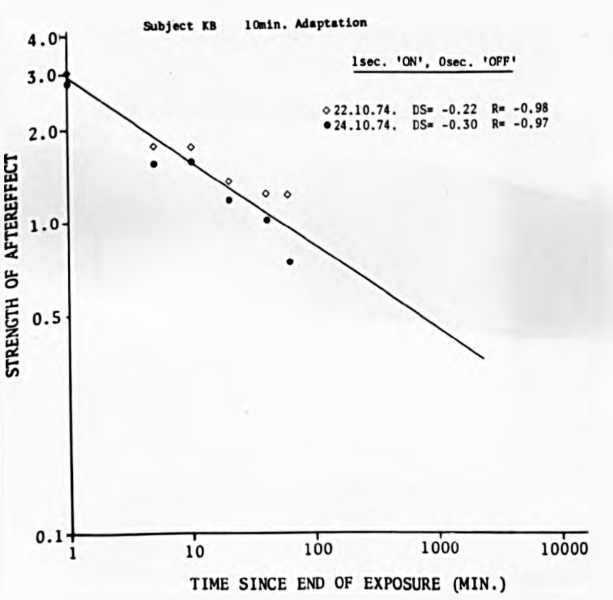
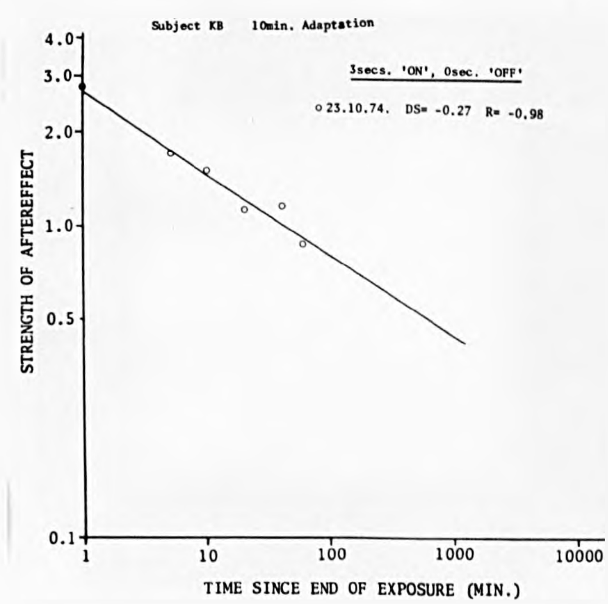


FIG. IX EXPERIMENTS WITH A 0 SEC. 'OFF' PERIOD









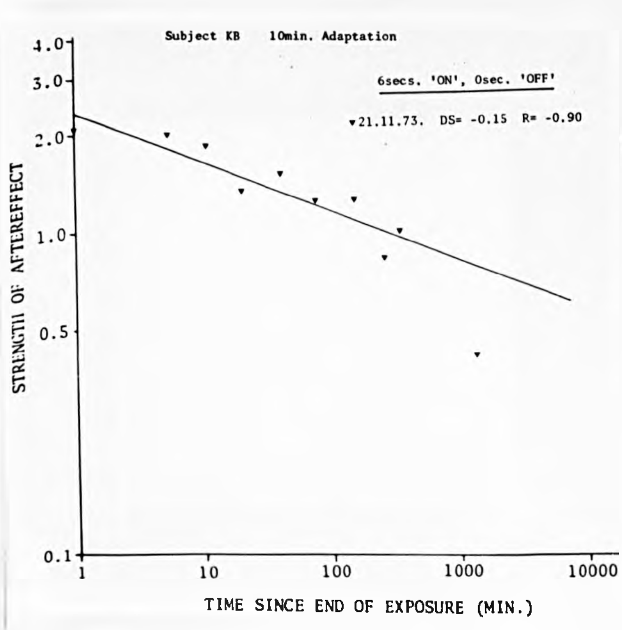
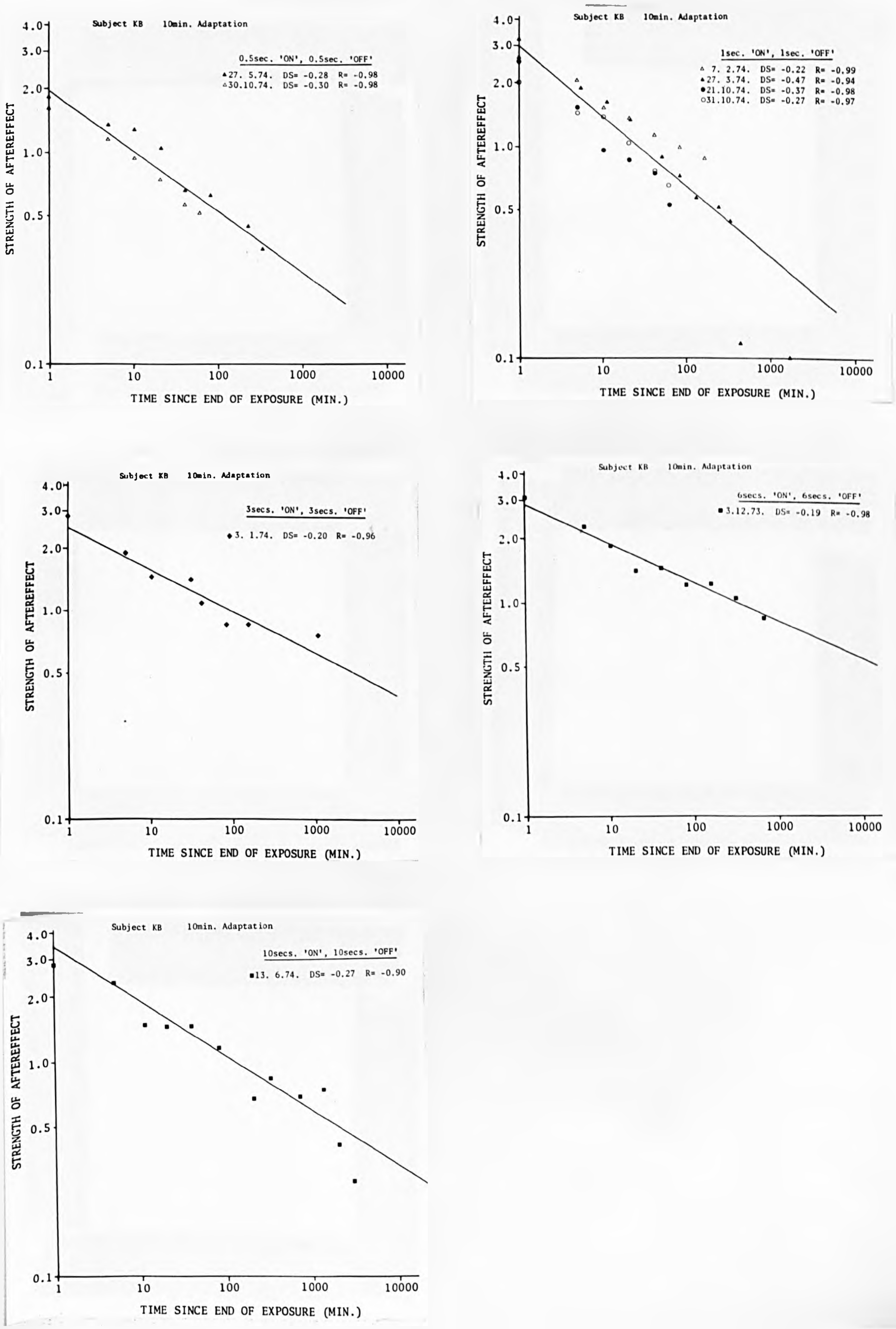


FIG. X EXPERIMENTS WITH EQUAL 'ON' AND 'OFF' PERIODS



The following Tables show the data derived from a statistical analysis of the exploratory experiments. The following abbreviations are used:

Time - time, in minutes, since the end of exposure

STR. - strength of A/E

B - slope of decay line, calculated using the equation:

$$b_{yx} = \frac{\Sigma XY - [(\Sigma X)(\Sigma Y)/N]}{\Sigma X^2 - [(\Sigma X)^2/N]}$$

R - Correlation coefficient, calculated using the equation:

$$r = \frac{N\Sigma XY - (\Sigma X)(\Sigma Y)}{\sqrt{[N\Sigma X^2 - (\Sigma X)^2][N\Sigma Y^2 - \Sigma Y)^2]}}$$

Y(1) - Estimated strength at time of first reading

Y(N) - Estimated strength at time of last reading

Both Y(1) and Y(N) are calculated using the equations:

$$A_{yx} = \bar{Y} - b_{yx} (\bar{x})$$

$$Y = a + bx$$

LOG/LOG ANALYSIS - logarithm taken of both time and strength values

LIN/LOG ANALYSIS - logarithm taken of only the time values

TEMPORAL SEQUENCE: 1 sec. ON | 10 sec. OFF

Subject KB

DURATION	DATE	START	FIRST READ TIME	FIRST READ STR.	LAST READ TIME	LAST READ STR.	LOG/LOG ANALYSIS B	LOG/LOG R	LOG/LOG Y(1)	LOG/LOG Y(N)	LIN/LOG ANALYSIS B	LIN/LOG R	LIN/LOG Y(1)	LIN/LOG Y(N)
44 sec.	21.8.74	9.40	1	0.4	5	0.2	-0.46	-1.00	0.4	0.2	-0.29	-1.00	0.4	0.2
6 min.	22.8.74	11.40	1	0.9	10	0.3	-0.49	-0.97	0.9	0.3	-0.65	-0.96	0.9	0.3
10 min.	5.2.74	1.45	1	1.8	80	0.3	-0.49	-0.97	1.7	0.3	-0.77	-0.93	1.6	0.1
10 min.	20.8.74	11.05	1	1.4	40	0.5	-0.30	-0.95	1.6	0.5	-0.61	-0.97	1.5	0.5
15 min.	25.3.74	3.00 }	1	2.6	320	0.2	-0.44	-0.99	3.1	0.3	-0.96	-0.97	2.4	-0.1
		}	1	2.6	81	0.2	-0.39	-0.99	2.8	0.5	-1.15	-0.98	2.5	0.3
15 min.	4.6.74	11.00 }	1	1.7	170	<0.1	-0.58	-0.90	2.3	0.1	-0.69	-0.96	1.5	<0.1
		}	1	1.7	88	0.3	-0.40	-0.96	1.7	0.3	-0.75	-0.95	1.6	0.1
15 min.	17.6.74	10.20 }	1	2.4	320	0.2	-0.43	-0.97	2.4	0.2	-0.82	-0.92	2.0	0.1
		}	1	2.4	80	0.5	-0.40	-0.98	2.3	0.4	-1.00	-0.94	2.1	0.2
20 min.	4.2.74	2.30	1	2.0	80	0.3	-0.42	-1.00	2.1	0.3	-0.88	-0.97	1.8	0.2
20 min.	21.5.74	11.00 }	1	2.2	300	0.1	-0.42	-0.96	2.1	0.2	-0.73	-0.91	1.7	0.1
		}	1	2.2	83	0.4	-0.39	-0.95	1.9	0.4	-0.90	-0.92	1.9	0.2
50 min.	5.6.74	10.00 }	1	3.3	160	<0.1	-0.47	-0.98	3.7	0.4	-1.35	-0.97	3.0	<0.1
		}	1	3.3	80	0.4	-0.43	-0.98	3.8	0.5	-1.88	-0.98	3.1	0.2
50 min.	6.6.74	10.30 }	1	3.6	620	0.2	-0.47	-0.98	3.9	0.2	-1.16	-0.93	2.9	0.3
		}	1	3.6	100	0.4	-0.49	-0.99	4.0	0.4	-1.65	-0.97	3.3	0.0
50 min.	22.6.74	10.40	1	3.3	80	0.3	-0.52	-0.95	4.1	0.4	-1.54	-0.99	3.1	0.2

TEMPORAL SEQUENC : 1sec. ON | 10 sec. OFF

Subject MY

DURATION	DATE	START	FIRST READ TIME	FIRST READ STR.	LAST READ TIME	LAST READ STR.	LOG/LOG ANALYSIS B	LOG/LOG ANALYSIS R	LOG/LOG ANALYSIS Y(1)	LOG/LOG ANALYSIS Y(N)	LIN/LOG ANALYSIS B	LIN/LOG ANALYSIS R	LIN/LOG ANALYSIS Y(1)	LIN/LOG ANALYSIS Y(N)
10 min.	19.2.74	10.40	1	1.1	200	0.1	-0.47	-0.98	1.4	0.1	-0.46	-0.97	1.1	0.0
			1	1.1	57	0.2	-0.42	-0.97	1.3	0.2	-0.55	-0.99	1.1	0.2
20 min.	4.6.74	10.00	1	2.1	220	0.2	-0.50	-0.97	1.8	0.1	-0.74	-0.87	1.6	0.0
			1	2.1	125	0.1	-0.58	-1.00	2.1	0.1	-0.88	-0.91	1.7	0.0
50 min	18.6.74	10.15	1	3.4	355	0.1	-0.63	-0.97	4.8	0.1	-1.22	-0.95	2.8	0.3
			1	3.4	100	0.3	-0.48	-0.99	3.7	0.4	-1.48	-0.96	3.0	0.1

TEMPORAL SEQUENCE: 1 sec. ON | 10 sec. OFF

Subject SRH

DURATION	DATE	START	FIRST READ TIME	FIRST READ STR.	LAST READ TIME	LAST READ STR.	LOG/LOG ANALYSIS B	LOG/LOG ANALYSIS R	LOG/LOG ANALYSIS Y(1)	LOG/LOG ANALYSIS Y(N)	LIN/LOG ANALYSIS B	LIN/LOG ANALYSIS R	LIN/LOG ANALYSIS Y(1)	LIN/LOG ANALYSIS Y(N)
10 min.	20.3.74	11.10	1	1.0	340	0.1	-0.47	-0.85	1.4	0.1	-0.37	-0.90	1.0	0.0
			1	1.0	81	0.1	-0.44	-0.89	1.3	0.2	-0.46	-0.92	1.0	0.2
10 min.	26.4.74	11.10	1	0.8	180	0.4	-0.96	-0.87	1.0	0.0	-0.39	-0.96	0.7	0.1
20 min.	31.5.74	11.15	1	0.9	270	0.2	-0.29	-0.94	0.9	0.2	-0.28	-0.92	0.8	0.1
			1	0.9	84	0.2	-0.27	-0.88	0.9	0.3	-0.31	-0.89	0.8	0.2
20 min.	13.6.74	11.00	1	0.8	150	0.2	-0.30	-0.92	1.0	0.2	-0.32	-0.93	0.9	0.2
			1	0.8	90	0.3	-0.27	-0.90	0.9	0.3	-0.32	-0.91	0.9	0.3
50 min.	7.6.74	11.15	1	2.0	165	0.1	-0.53	-0.95	3.0	0.2	-0.88	-0.99	2.0	0.0
			1	2.0	80	0.3	-0.43	-0.96	2.4	0.4	-0.91	-1.00	2.0	0.3

TEMPORAL SEQUENCE : 10 sec. ON | 1 sec. OFF .

Subject KB

DURATION	DATE	START	FIRST READ TIME	FIRST READ STR.	LAST READ TIME	LAST READ STR.	LOG/LOG ANALYSIS B	LOG/LOG ANALYSIS R	LOG/LOG ANALYSIS Y(1)	LOG/LOG ANALYSIS Y(N)	LIN/LOG ANALYSIS B	LIN/LOG ANALYSIS R	LIN/LOG ANALYSIS Y(1)	LIN/LOG ANALYSIS Y(N)
44 sec.	26.6.74	10.30	1	0.5	86	0.4	-0.11	-0.75	0.5	0.3	-0.11	-0.76	0.5	0.3
88 sec.	25.6.74	10.15	1	0.6	150	0.3	-0.12	-0.74	0.7	0.4	-0.13	-0.74	0.7	0.4
			1	0.6	80	0.4	-0.09	-0.62	0.7	0.5	-0.10	-0.59	0.7	0.5
3 min.	19.8.74	10.40	1	1.8	445	0.5	-0.20	-0.96	2.0	0.6	-0.46	-0.99	1.8	0.5
			1	1.8	80	1.0	-0.14	-0.99	1.8	0.9	-0.43	-0.99	1.7	0.9
6 min.	23.8.74	10.25	1	2.1	630	0.7	-0.20	-0.94	2.7	0.8	-0.63	-0.93	2.4	0.7
			1	2.1	80	1.1	-0.14	-0.84	2.5	1.3	-0.55	-0.83	2.4	1.3
10 min.	6.2.74	11.05	1	2.8	320	0.7	-0.23	-0.98	2.8	0.8	-0.79	-0.97	2.6	0.6
			1	2.8	80	1.0	-0.23	-0.97	2.8	1.0	-0.93	-0.97	2.7	0.9
10 min.	29.3.74	12.45	1	2.9	4800	0.2	-0.29	-0.96	3.9	0.3	-0.72	-0.98	2.8	0.1
10 min.	7.6.74	10.15	1	2.7	1700	0.1	-0.36	-0.79	4.4	0.3	-0.73	-0.98	2.7	0.3
			1	2.7	95	1.3	-0.15	-0.96	2.6	1.4	-0.67	-0.95	2.6	1.3
10 min.	23.6.74	11.30	1	2.9	245	0.9	-0.21	-0.95	3.5	1.1	-0.97	-0.98	3.1	1.0
			1	2.9	80	1.5	-0.15	-0.95	3.1	1.6	-0.76	-0.96	3.0	1.6
10 min.	12.10.7		1	2.7	92	1.0	-0.20	-0.97	2.8	1.1	-0.84	-0.99	2.7	1.1

10 sec. OFF / ON · VARIED.   10 MIN. EXPOSURE

Subject KB

SEQUENCE	DATE	START	FIRST READ		LAST READ		LOG/LOG ANALYSIS				LIN/LOG ANALYSIS			
			TIME	STR.	TIME	STR.	B	R	Y(1)	Y(N)	B	R	Y(1)	Y(N)
1 sec. ON	5.2.74	1.45	1	1.8	80	0.3	-0.40	-0.97	1.7	0.3	-0.77	-0.93	1.6	0.1
1 sec. ON	20.8.74	11.15	1	1.4	40	0.5	-0.30	-0.95	1.6	0.5	-0.60	-0.97	1.5	0.5
2 sec. ON	20.6.74	10.10	1	1.6	80	0.1	-0.57	-0.86	2.3	0.2	-0.76	-0.99	1.6	0.2
2 sec. ON	5.8.74	10.30	1	1.7	80	0.1	-0.57	-0.92	2.4	0.2	-0.84	-0.99	1.7	0.1
2 sec. ON	8.8.74	10.00	1	1.3	72	0.3	-0.33	-0.91	1.5	0.4	-0.50	-0.97	1.3	0.3
3 sec. ON	19.6.74	11.05 }	1	2.3	1360	0.2	-0.33	-0.98	2.7	0.3	-0.64	-0.98	2.0	0.0
		}	1	2.3	77	0.7	-0.26	-0.99	2.3	0.8	-0.80	-0.99	2.[illegible]	0.7
3 sec. ON	7.8.74	10.15 }	1	1.8	165	0.3	-0.37	-0.98	2.1	0.3	-0.70	-0.99	1.7	0.2
		}	1	1.8	80	0.4	-0.35	-0.97	2.0	0.4	-0.74	-0.99	1.8	0.4
3 sec. ON	14.8.74	10.45 }	1	2.6	140	0.5	-0.34	-0.96	3.2	0.6	-1.02	-0.98	2.7	0.5
		}	1	2.6	75	0.8	-0.28	-0.97	2.9	0.9	-1.02	-0.97	2.7	0.8
5 sec. ON	15.10.74	10.30	1	1.5	60	0.4	-0.34	-0.95	1.8	0.5	-0.65	-0.98	1.6	0.4
10 sec. ON	13.6.74	10.10 }	1	2.8	2900	0.3	-0.26	-0.95	3.2	0.4	-0.67	-0.96	2.5	0.2
		}	1	2.8	80	1.1	-0.21	-0.95	2.9	1.2	-0.91	-0.95	2.8	1.0

TEMPORAL SEQUENCE : 5 sec. ON | ½ sec. OFF

Subjects KB + SRH

DURATION	DATE	START	FIRST READ TIME	FIRST READ STR.	LAST READ TIME	LAST READ STR.	LOG/LOG ANALYSIS B	LOG/LOG ANALYSIS R	LOG/LOG ANALYSIS Y(1)	LOG/LOG ANALYSIS Y(N)	LIN/LOG ANALYSIS B	LIN/LOG ANALYSIS R	LIN/LOG ANALYSIS Y(1)	LIN/LOG ANALYSIS Y(N)
10 min.	2.5.74	9.45	1	4.0	6000	0.1	-0.39	-0.92	6.8	0.2	-0.98	-0.99	3.6	0.0
Subj. KB			1	4.0	91	1.7	-0.21	-0.99	4.1	1.6	-1.30	-0.99	3.9	1.5
10 min.	14.5.77	11.25	1	2.2	1400	0.3	-0.37	-0.95	2.0	0.3	-0.55	-0.89	1.8	0.0
Subj. SRH			1	2.2	90	0.6	-0.30	-0.91	2.1	0.5	-0.82	-0.90	2.0	0.4

TEMPORAL SEQUENCE : 1/2 sec. ON | 5 sec. OFF

Subject: KB

DURATION	DATE	START	FIRST READ		LAST READ		LOG/LOG ANALYSIS				LIN/LOG ANALYSIS			
			TIME	STR.	TIME	STR.	B	R	Y(1)	Y(N)	B	R	Y(1)	Y(N)
10 min.	22.4.74	11.00	1	1.2	300	0.1	-0.51	-0.92	1.8	0.1	-0.50	-0.94	1.2	0.0
			1	1.2	100	0.1	-0.49	-0.90	1.7	0.2	-0.56	-0.93	1.3	0.1
15 min.	25.4.74	10.00	1	1.9	340	0.1	-0.64	-0.89	2.6	0.1	-0.72	-0.95	1.6	0.2
			1	1.9	78	0.1	-0.67	-0.91	2.8	0.2	-0.94	-1.00	1.8	0.0
50 min.	11.6.74	10.10	1	3.5	200	0.2	-0.49	-0.98	4.5	0.3	-1.37	-0.97	3.2	0.0
			1	3.5	90	0.6	-0.40	-0.99	3.9	0.7	-1.54	-0.99	3.3	0.4

TEMPORAL SEQUENCE : ½ sec. ON / 5 sec. OFF

Subject SRH

DURATION	DATE	START	FIRST READ		LAST READ		LOG/LOG ANALYSIS				LIN/LOG ANALYSIS			
			TIME	STR.	TIME	STR.	B	R	Y(1)	Y(N)	B	R	Y(1)	Y(N)
10 min.	22.4.74	10.30	1	0.8	170	0.1	-0.51	-0.91	1.1	0.1	-0.35	-0.94	0.8	0.0
15 min.	30.4.74	11.30	1.	1.0	270	0.2	-0.38	-0.94	1.1	0.1	-0.39	-0.92	1.0	0.0

10 sec. ON | OFF · VARIED   10 MIN. EXPOSURE

Subject KB

SEQUENCE	DATE	START	FIRST READ TIME	FIRST READ STR.	LAST READ TIME	LAST READ STR.	LOG/LOG ANALYSIS B	LOG/LOG R	LOG/LOG Y(1)	LOG/LOG Y(N)	LIN/LOG ANALYSIS B	LIN/LOG R	LIN/LOG Y(1)	LIN/LOG Y(N)
1 sec. OFF	6.2.74	11.05	1	2.8	320	0.7	-0.27	-0.98	2.8	0.8	-0.79	-0.97	2.6	0.6
			1	2.8	90	1.0	-0.23	-0.97	2.8	1.0	-0.93	-0.97	2.7	0.9
1 sec. OFF	29.3.74	12.45	1	2.9	4800	0.2	-0.29	-0.96	3.9	0.3	-0.72	-0.98	2.8	0.1
1 sec. OFF	7.6.74	10.15	1	2.7	1700	0.1	-0.36	-0.79	4.4	0.5	-0.73	-0.98	2.7	0.3
			1	2.7	95	1.3	-0.15	-0.96	2.6	1.4	-0.67	-0.95	2.6	1.3
1 sec. OFF	23.6.74	11.30	1	2.9	245	0.9	-0.21	-0.95	3.5	1.1	-0.87	-0.98	3.1	1.0
			1	2.9	80	1.5	-0.15	-0.95	3.1	1.6	-0.76	-0.96	3.0	1.6
1 sec. OFF	12.10.74	10.45	1	2.7	92	1.0	-0.20	-0.97	2.9	1.1	-0.84	-0.99	2.7	1.1
5 sec. OFF	19.10.74	10.45	1	2.7	60	1.1	-0.22	-1.00	2.7	1.1	-0.91	-0.98	2.6	1.0
10 sec. OFF	13.6.74	10.10	1	2.8	2900	0.3	-0.26	-0.95	3.2	0.4	-0.67	-0.96	2.5	0.2
			1	2.8	80	1.1	-0.21	-0.95	2.9	1.2	-0.91	-0.95	2.8	1.0

10 sec. ON | OFF VARIED   10 min. EXPOSURE

Subjects MY, CMJ

SEQUENCE	DATE	START	FIRST READ TIME	FIRST READ STR.	LAST READ TIME	LAST READ STR.	LOG/LOG ANALYSIS B	LOG/LOG R	LOG/LOG Y(1)	LOG/LOG Y(N)	LIN/LOG ANALYSIS B	LIN/LOG R	LIN/LOG Y(1)	LIN/LOG Y(N)
1sec. OFF	6.2.74	1.30	1	2.1	1280	0.6	-0.16	-0.82	1.9	0.6	-0.43	-0.83	1.8	0.5
Subj. MY			1	2.1	81	0.7	-0.27	-0.98	2.4	0.7	-0.80	-1.00	2.2	0.6
1sec. OFF	19.3.74	11.00	1	2.5	2800	0.1	-0.19	-0.98	2.4	0.6	-0.57	-0.95	2.2	0.4
Subj. MY			1	2.5	81	1.0	-0.20	-0.97	2.5	1.0	-0.77	-0.97	2.4	0.9
1sec. OFF	22.2.74	11.00	1	1.3	640	0.2	-0.24	-0.82	1.5	0.4	-0.31	-0.89	1.3	0.4
Subj. CMJ			1	1.3	80	0.8	-0.12	-0.70	1.2	0.8	-0.26	-0.74	1.2	0.8
1sec. OFF	28.10.74	10.00	1	1.8	60	1.0	-0.15	-0.97	1.8	1.0	-0.47	-0.97	1.8	1.0
Subj. CMT														

ON = OFF : 10 MIN. EXPOSURE

Subject KB

SEQUENCE	DATE	START	FIRST READ		LAST READ		LOG/LOG ANALYSIS				LIN/LOG ANALYSIS			
			TIME	STR.	TIME	STR.	B	R	Y(1)	Y(N)	B	R	Y(1)	Y(N)
½ sec./½ sec.	27.5.74	2.40	1	1.8	330	0.4	-0.28	-0.98	2.1	0.4	-0.59	-0.99	1.8	0.3
			1	1.8	80	0.6	-0.26	-0.96	2.0	0.7	-0.65	-0.97	1.8	0.6
½ sec./½ sec.	30.10.74	10.50	1	1.6	60	0.5	-0.30	-0.98	1.8	0.5	-0.66	-0.99	1.6	0.5
1 sec./1 sec.	7.2.74	7.15pm	1	2.6	160	0.9	-0.22	-0.99	2.7	0.9	-0.81	-0.98	2.5	0.8
			1	2.6	80	1.1	-0.23	-0.99	2.7	1.0	-0.90	-0.98	2.6	0.9
1 sec./1 sec.	27.3.74	1.45	1	3.2	1860	0.1	-0.47	-0.94	4.7	0.1	-0.95	-0.96	2.7	0.4
			1	3.2	81	0.7	-0.34	-0.99	3.4	0.8	-1.30	-0.99	3.1	0.6
1 sec./1 sec.	21.10.74	9.55	1	2.5	60	0.5	-0.37	-0.98	2.6	0.6	-1.09	-0.97	2.4	0.4
1 sec./1 sec.	31.10.74	10.05	1	2.0	60	0.7	-0.27	-0.97	2.2	0.7	-0.77	-0.99	2.0	0.7
3 sec./3 sec.	3.1.74	3.45	1	2.9	1080	0.8	-0.20	-0.96	2.5	0.6	-0.68	-0.91	2.4	0.3
			1	2.9	80	0.9	-0.27	-0.99	2.9	0.9	-1.03	-0.98	2.7	0.7
6 sec./6 sec.	3.12.74	9.45	1	3.1	640	0.8	-0.19	-0.98	2.9	0.9	-0.73	-0.95	2.7	0.7
			1	3.1	80	1.2	-0.21	-0.99	3.1	1.2	-1.00	-0.97	3.0	1.0
10 sec./10 sec.	13.6.74	10.10	1	2.8	2900	0.3	-0.27	-0.95	3.2	0.4	-0.67	-0.96	2.5	0.2
			1	2.8	80	1.1	-0.21	-0.95	2.9	1.1	-0.91	-0.95	2.8	1.0

0 sec. OFF / ON VARIED   10 min. EXPOSURE

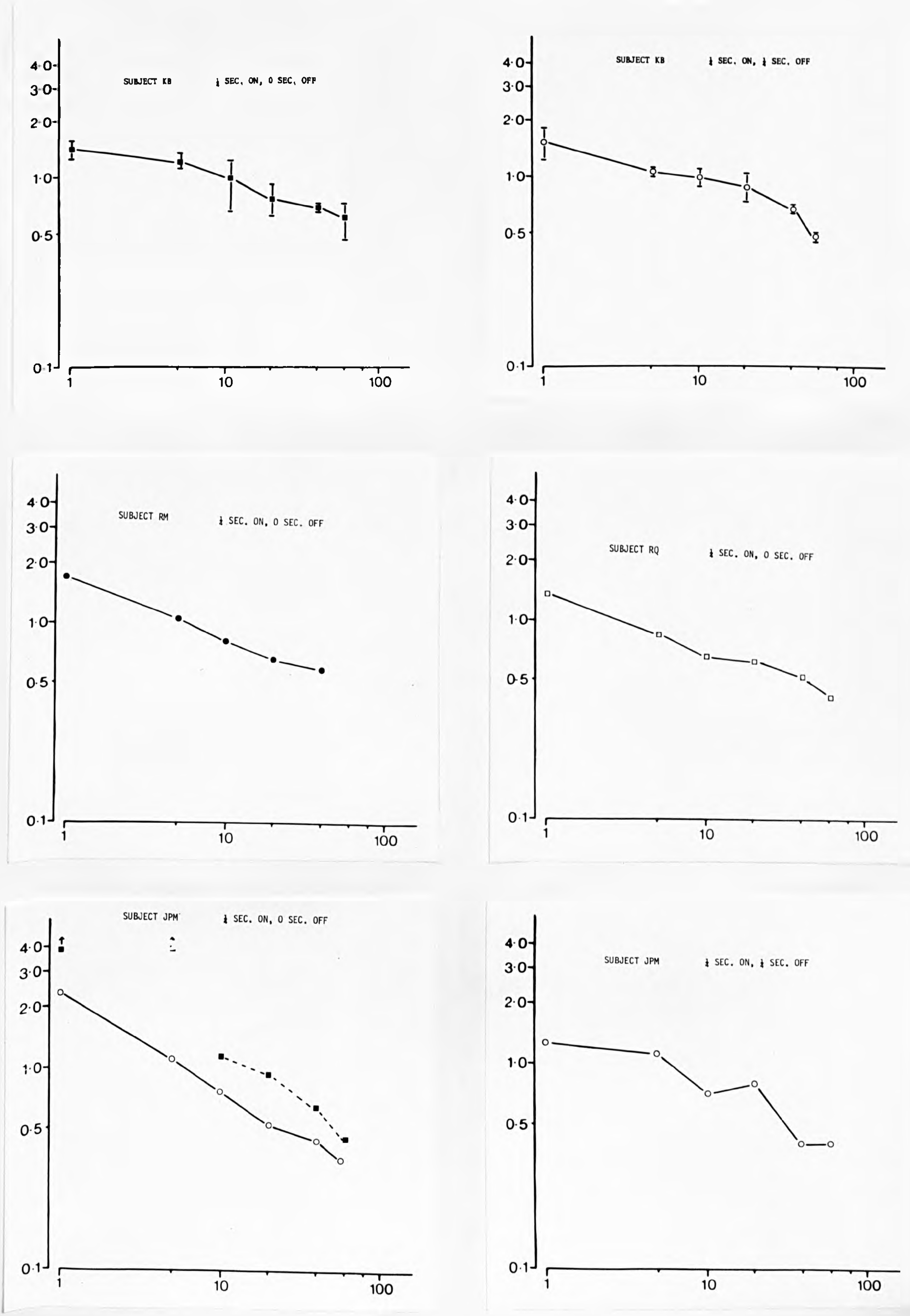
Subject KB

SEQUENCE	DATE	START	FIRST READ TIME	FIRST READ STR.	LAST READ TIME	LAST READ STR.	LOG/LOG ANALYSIS B	LOG/LOG ANALYSIS R	LOG/LOG ANALYSIS Y(1)	LOG/LOG ANALYSIS Y(N)	LIN/LOG ANALYSIS B	LIN/LOG ANALYSIS R	LIN/LOG ANALYSIS Y(1)	LIN/LOG ANALYSIS Y(N)
0.1 sec. ON	26.10.74	11.45	1	1.1	20	0.5	-0.27	-0.97	1.1	0.5	-0.47	-0.98	1.1	0.5
0.5 sec. ON	25.10.74	10.30	1	2.4	40	1.0	-0.23	-0.99	2.4	1.0	-0.85	-0.99	2.3	1.0
1 sec. ON	22.10.74	10.10	1	3.0	60	1.2	-0.22	-0.98	2.9	1.1	-0.99	-0.95	2.8	1.0
1 sec. ON	24.10.74	10.45	1	2.8	60	0.7	-0.30	-0.97	2.8	0.8	-1.08	-0.97	2.6	0.7
3 sec. ON	23.10.74	10.40	1	2.8	60	0.9	-0.27	-0.98	2.8	0.9	-1.04	-0.98	2.7	0.8
6 sec. ON	21.11.73	4.45	1	2.1	1400	0.4	-0.20	-0.89	2.7	0.6	-0.54	-0.95	2.3	0.6
			1	2.1	72	1.3	-0.12	-0.97	2.3	1.3	-0.48	-0.89	2.2	1.3

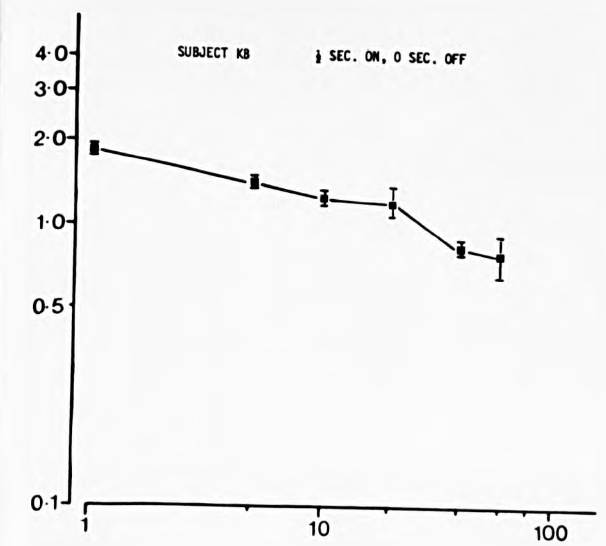
APPENDIX G. RESULTS OF A PARAMETRIC STUDY OF THE EFFECTS OF TEMPORAL PARAMETERS OF STIMULATION ON STRENGTH AND DECAY OF THE MCCOLLOUGH EFFECT.

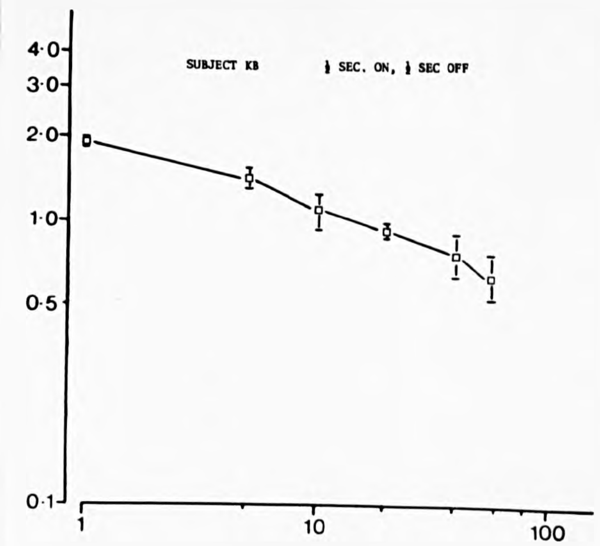
In all figures, the Y axis is the strength of the aftereffect (log. scale), and the X axis is the time, in seconds, since the end of adaptation (log. scale).

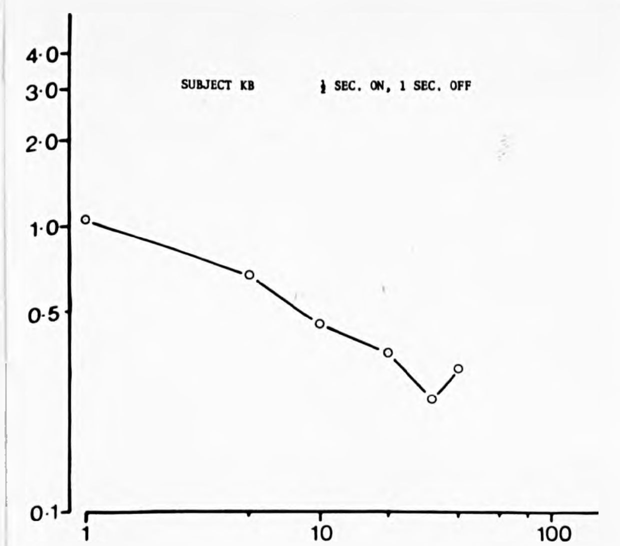
EXPERIMENTS WITH A $\frac{1}{4}$ SEC. 'ON' PERIOD

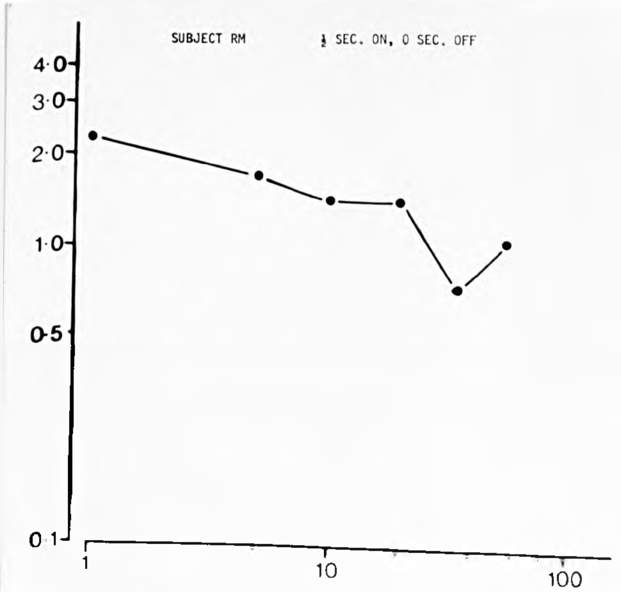


EXPERIMENTS WITH A ½ SEC. 'ON' PERIOD

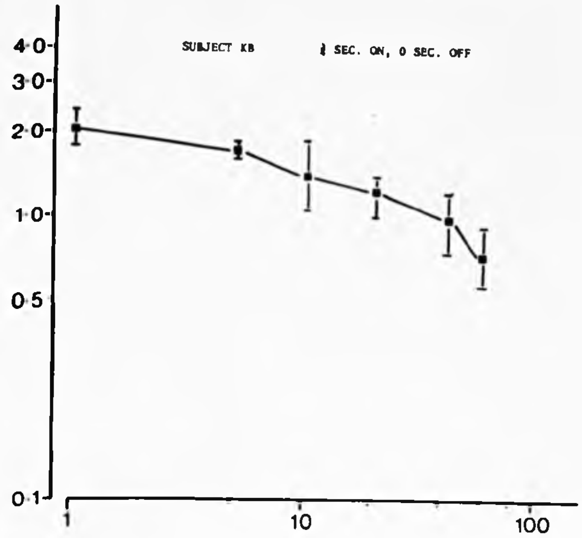


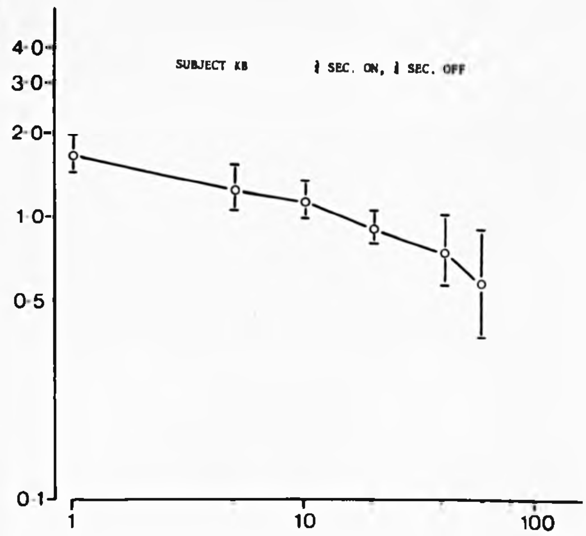


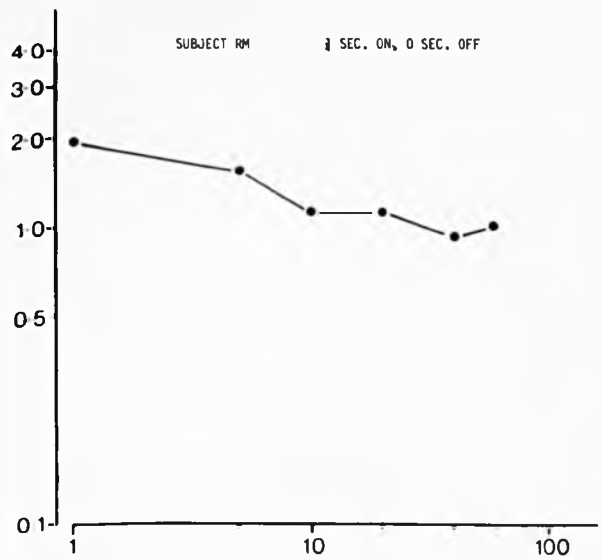




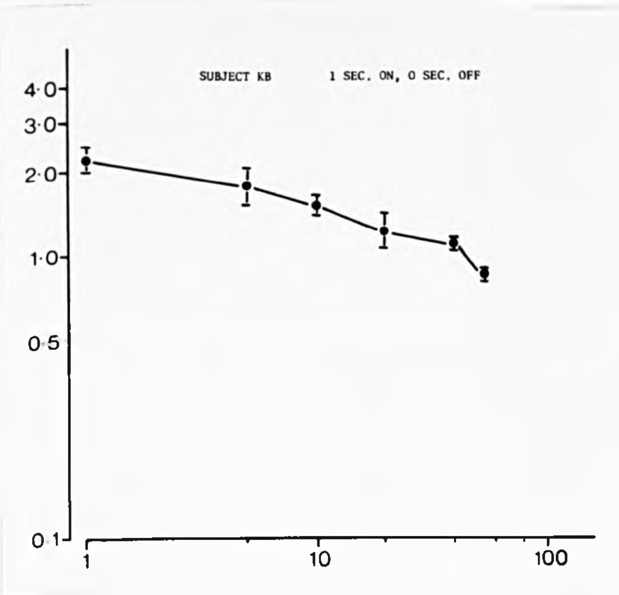
EXPERIMENTS WITH A ¾ SEC. 'ON' PERIOD

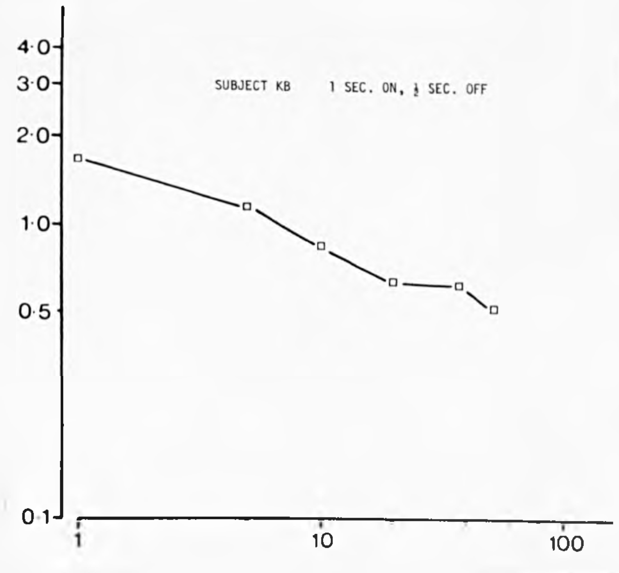


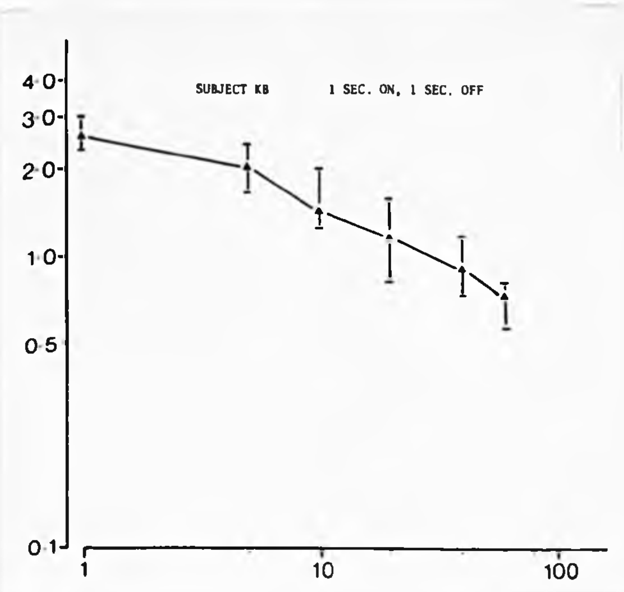


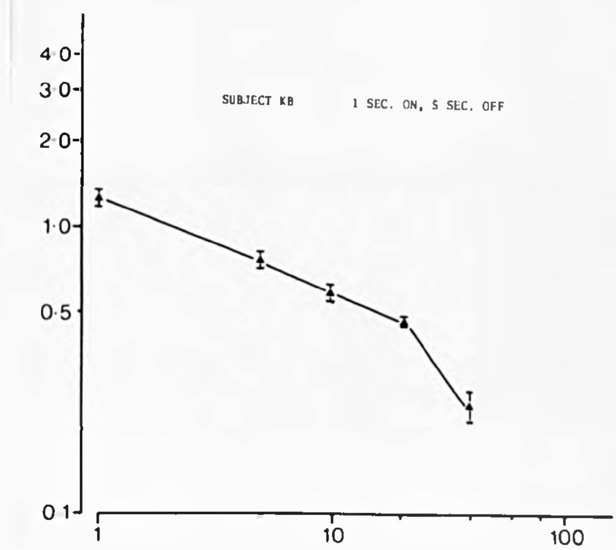


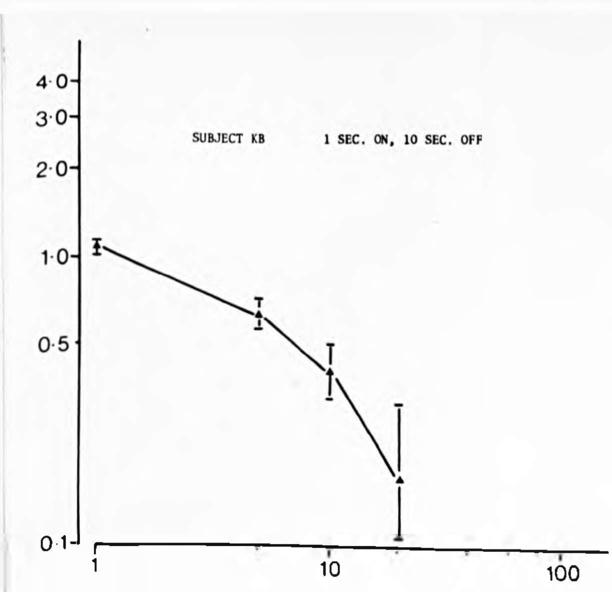
EXPERIMENTS WITH A 1 SEC. 'ON' PERIOD



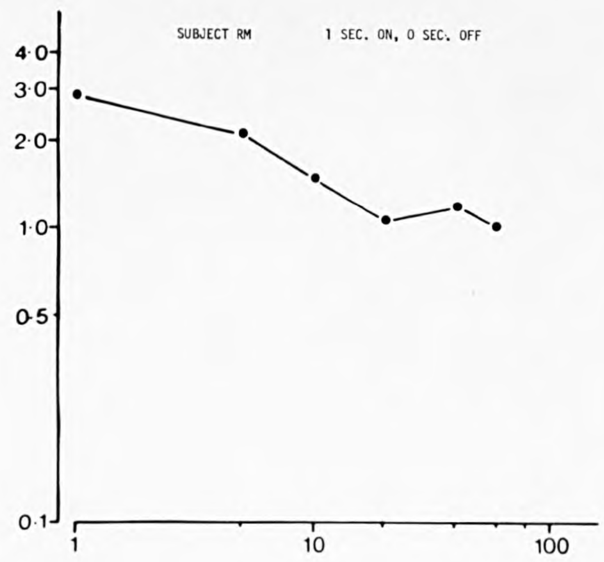


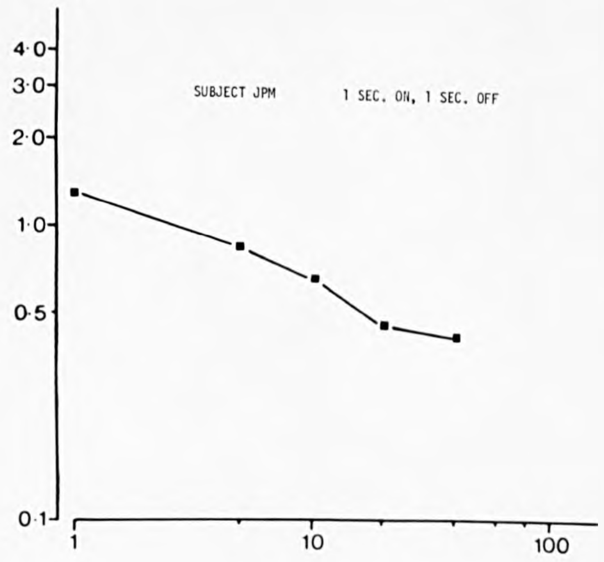


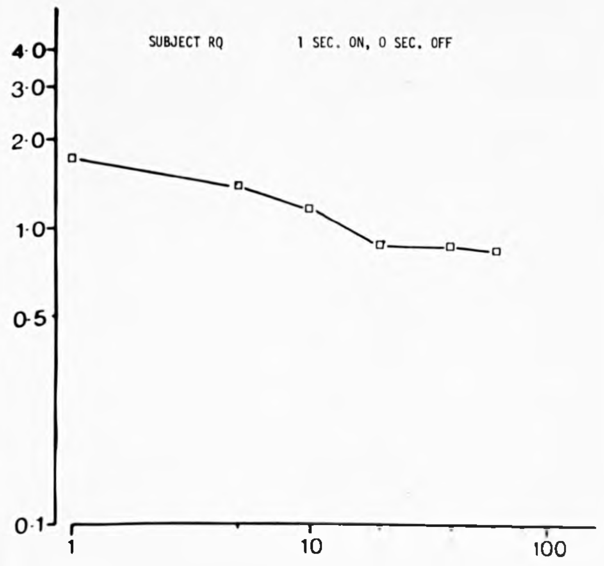




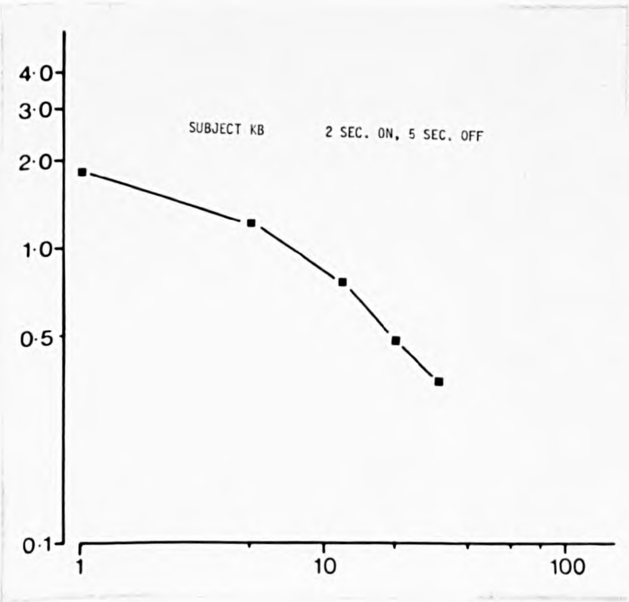
EXPERIMENTS WITH A 1 SEC. 'ON' PERIOD

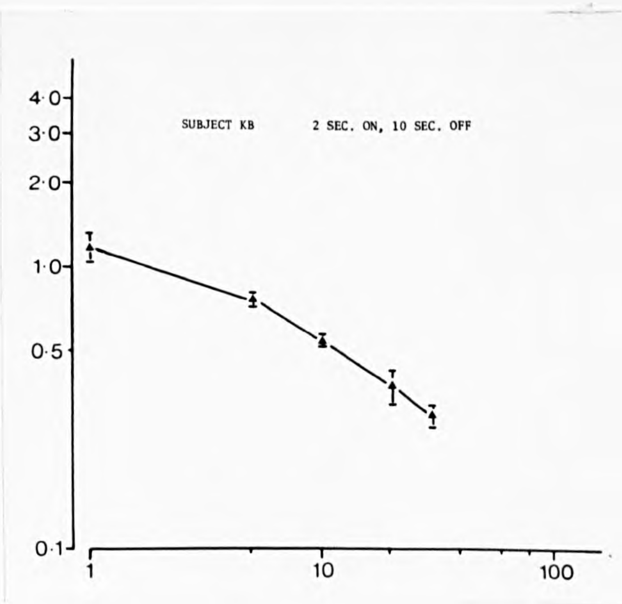




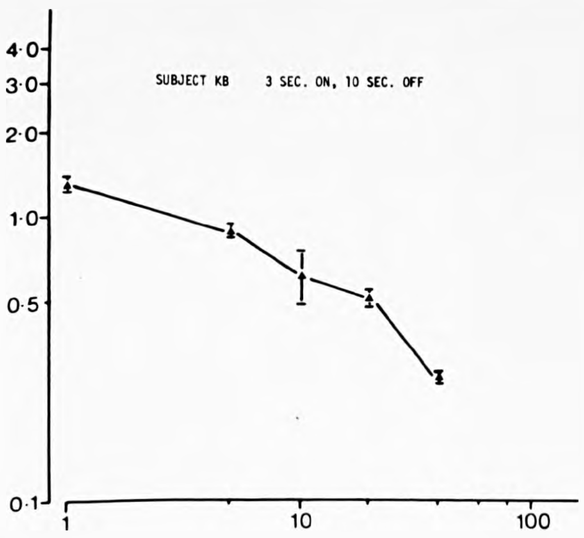


EXPERIMENTS WITH A 2 SEC. 'ON' PERIOD

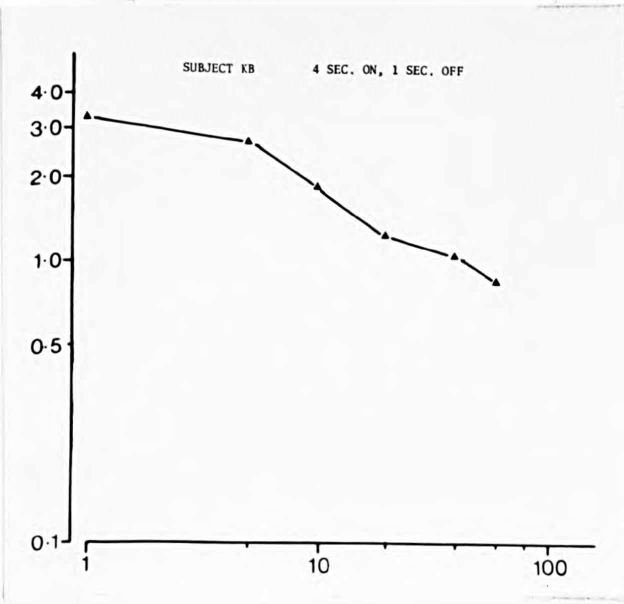


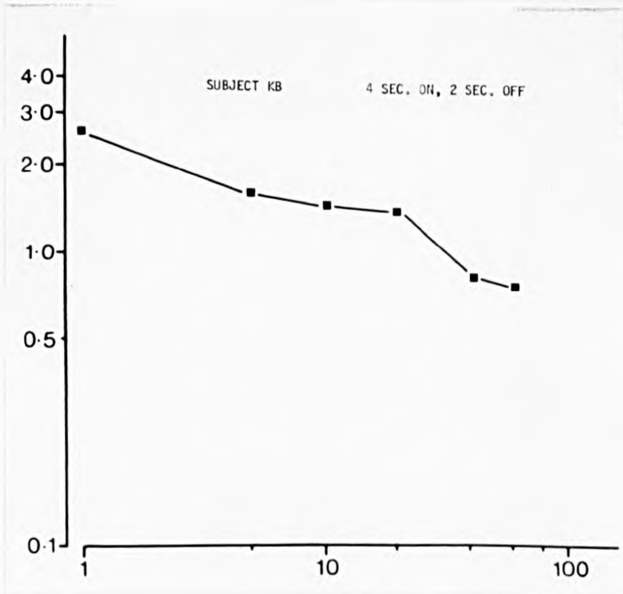


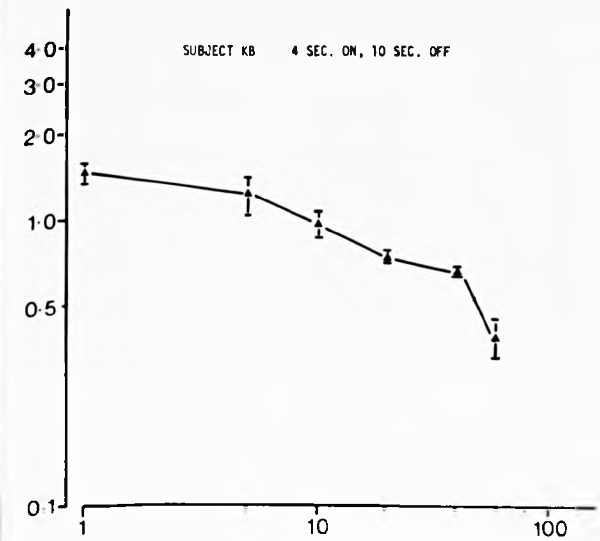
EXPERIMENTS WITH A 3 SEC. 'ON' PERIOD



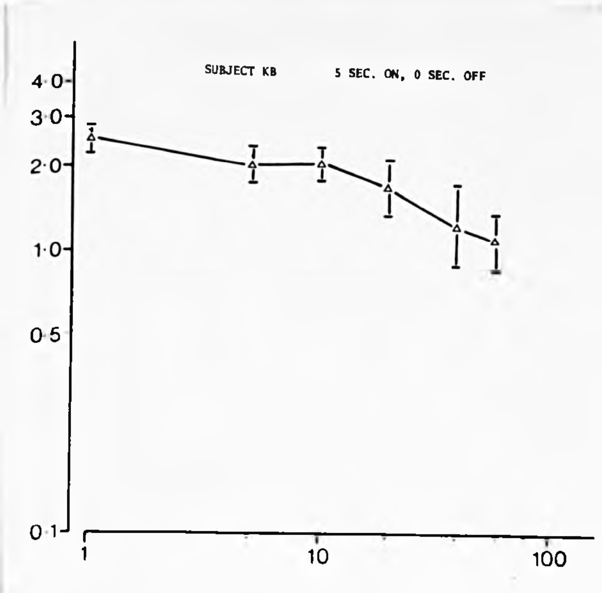
EXPERIMENTS WITH A 4 SEC. 'ON' PERIOD

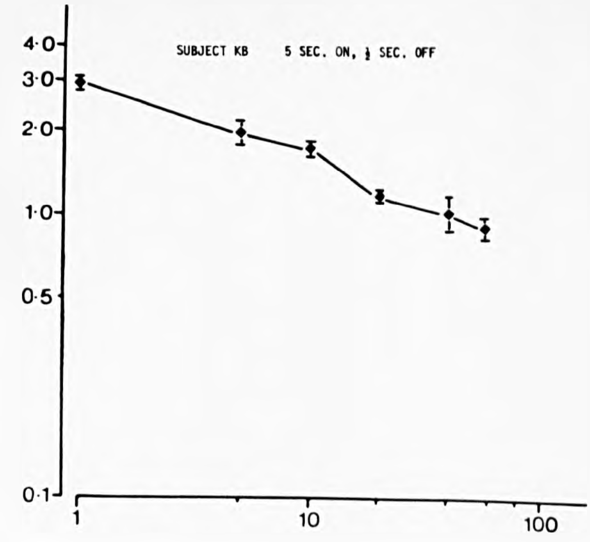


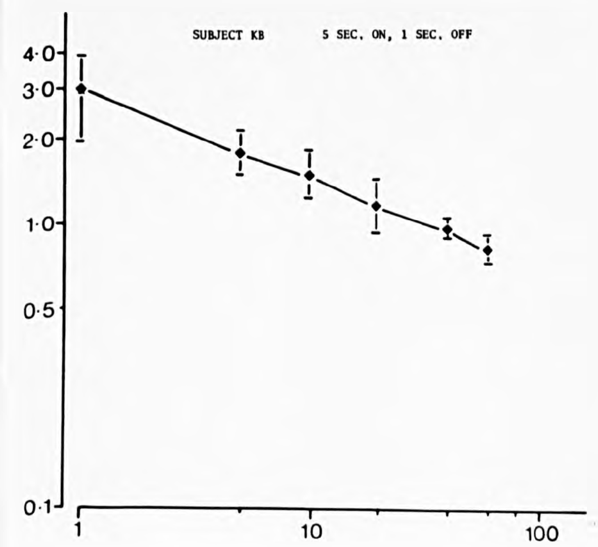


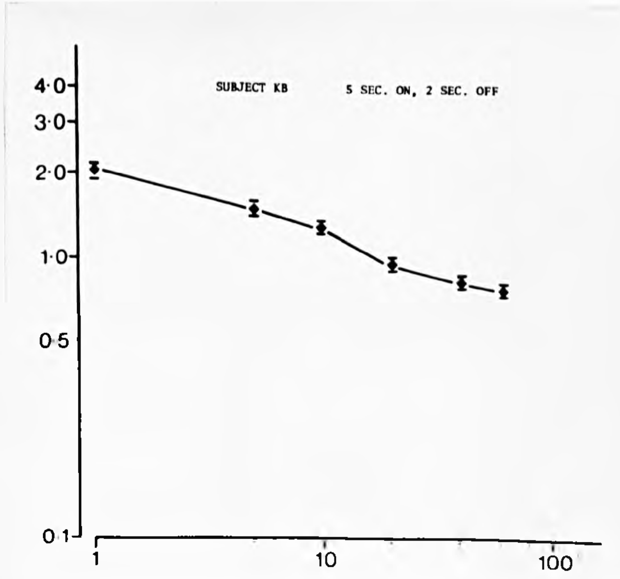


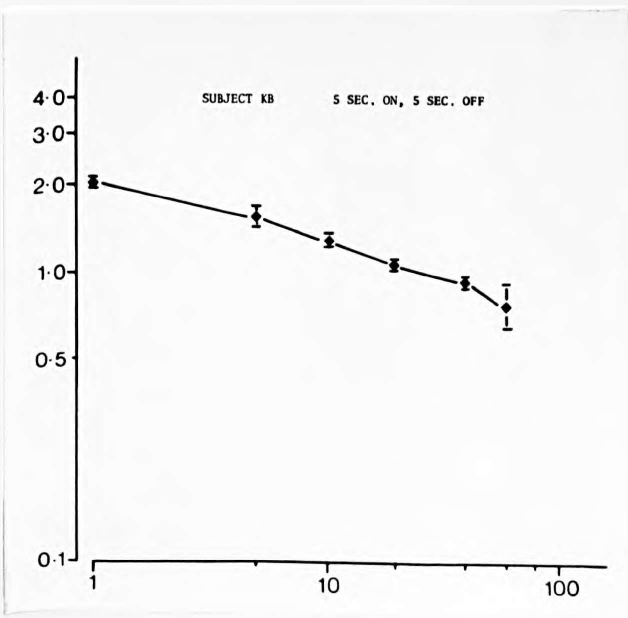
EXPERIMENTS WITH A 5 SEC. 'ON' PERIOD

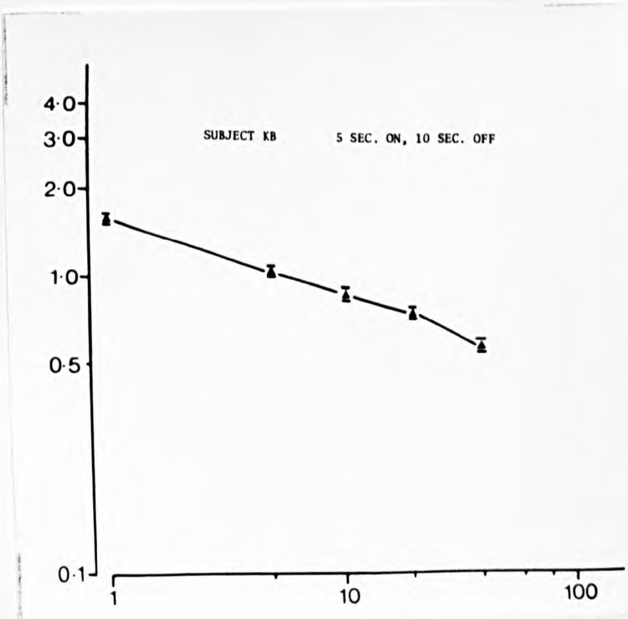




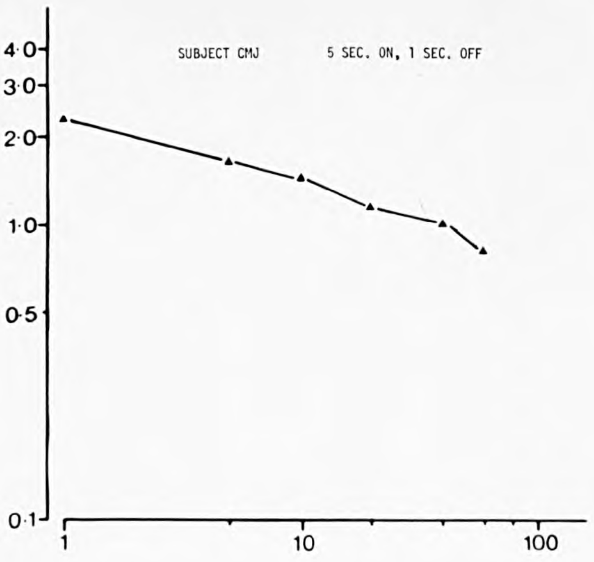


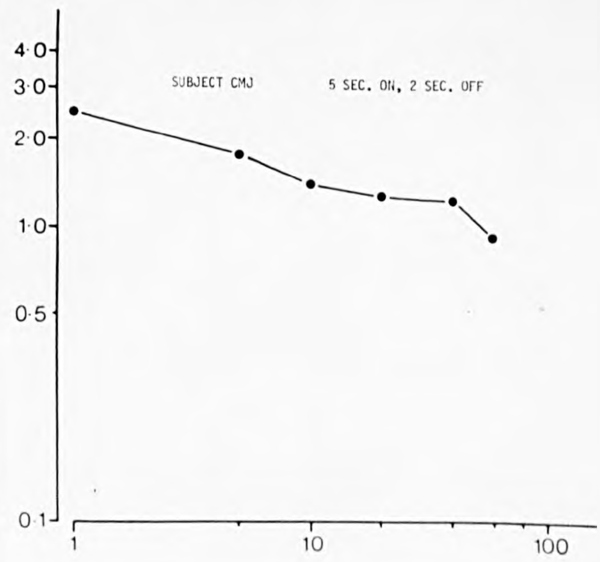


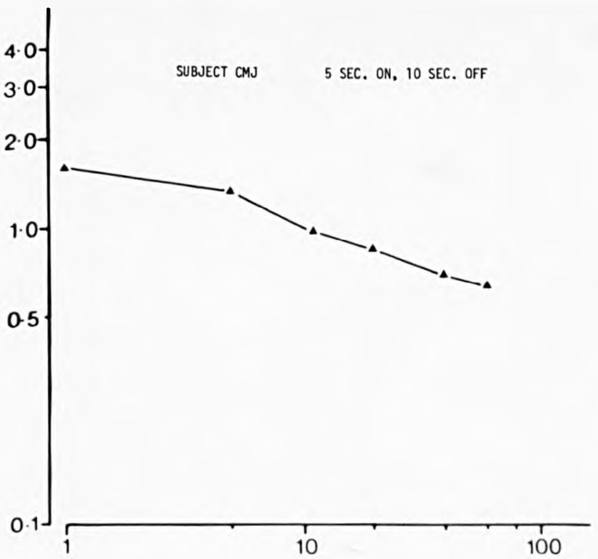


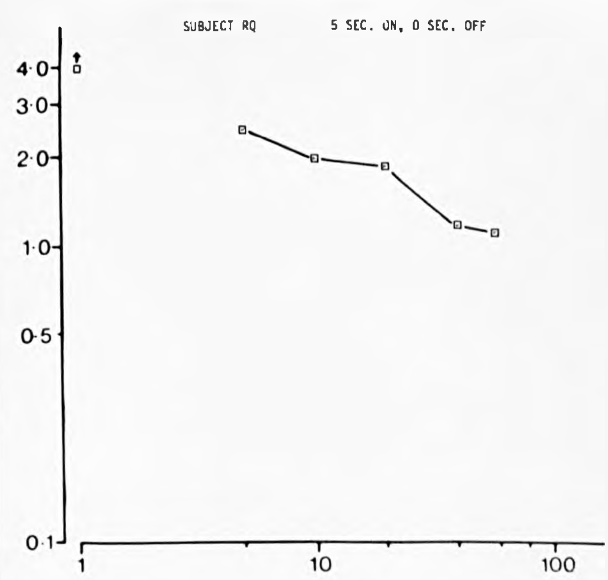


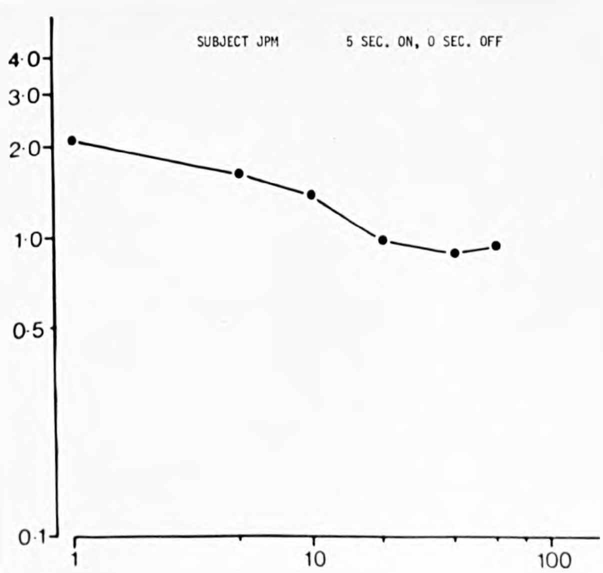
EXPERIMENTS WITH A 5 SEC. 'ON' PERIOD

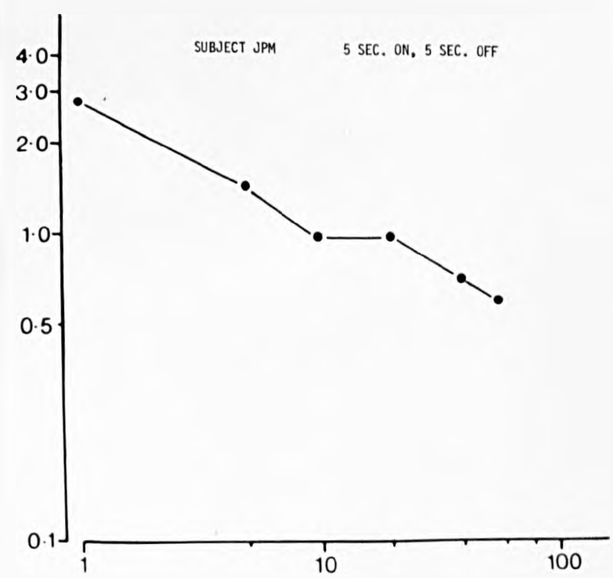




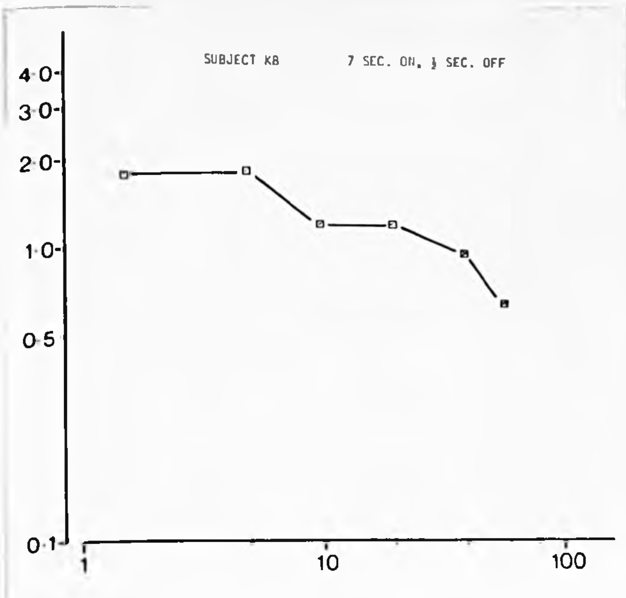


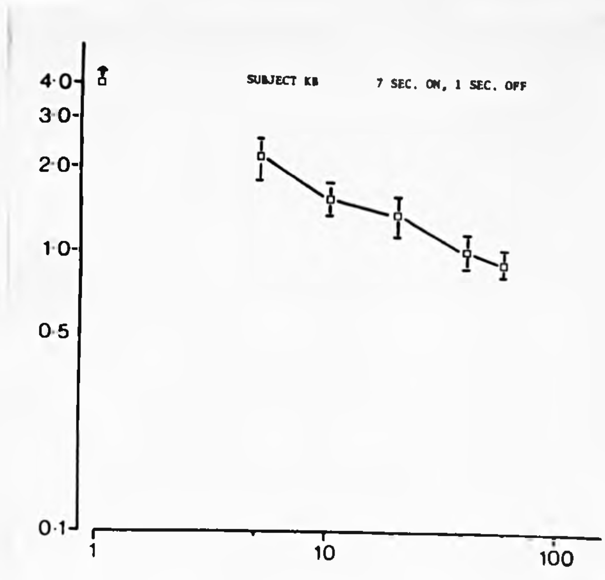




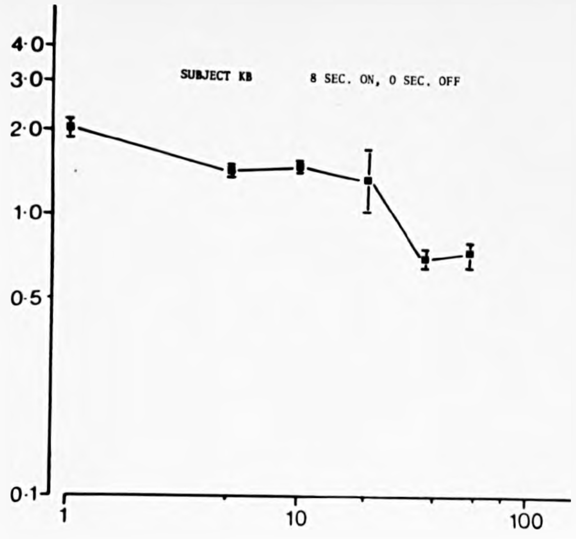


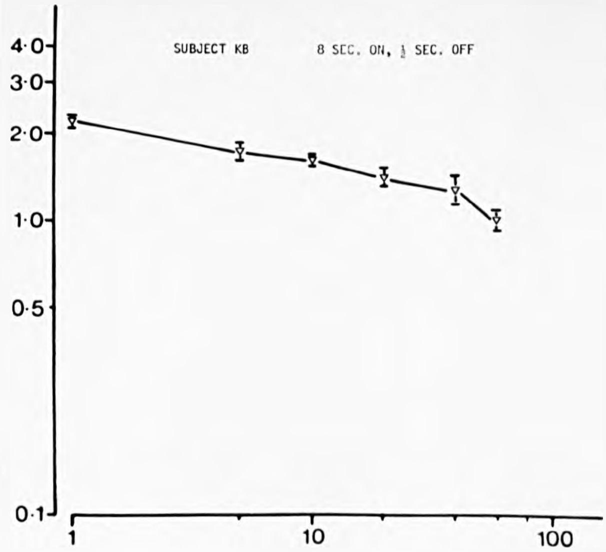
EXPERIMENTS WITH A 7 SEC. 'ON' PERIOD

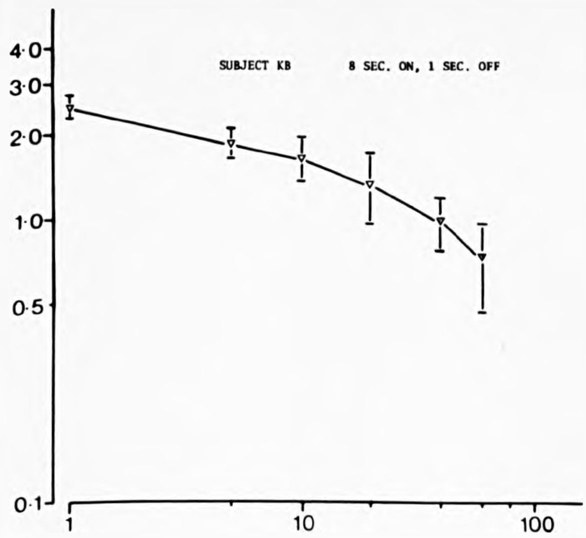


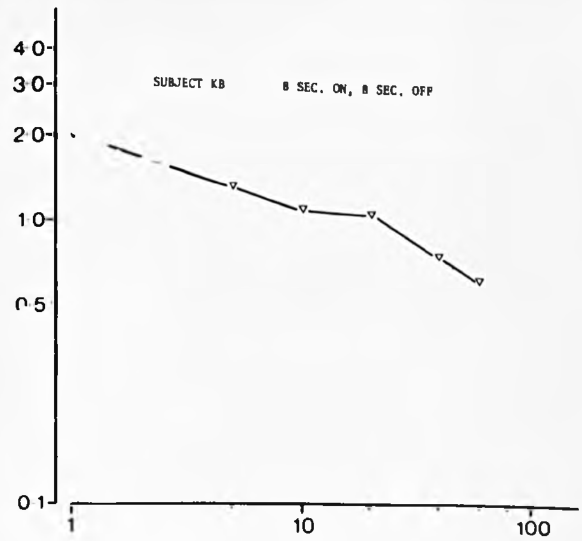


EXPERIMENTS WITH A 8 SEC. 'ON' PERIOD

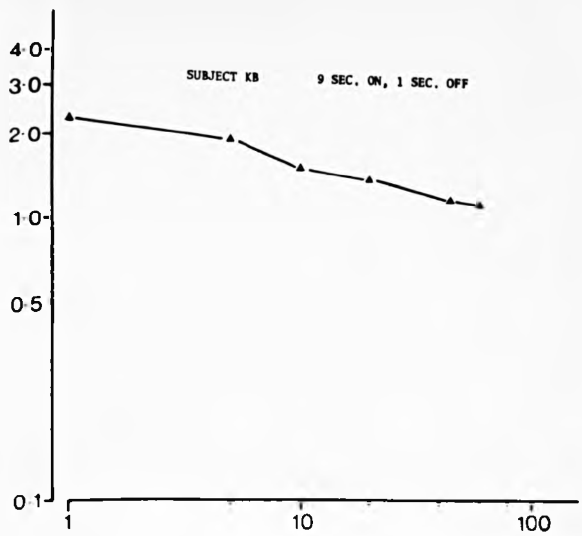




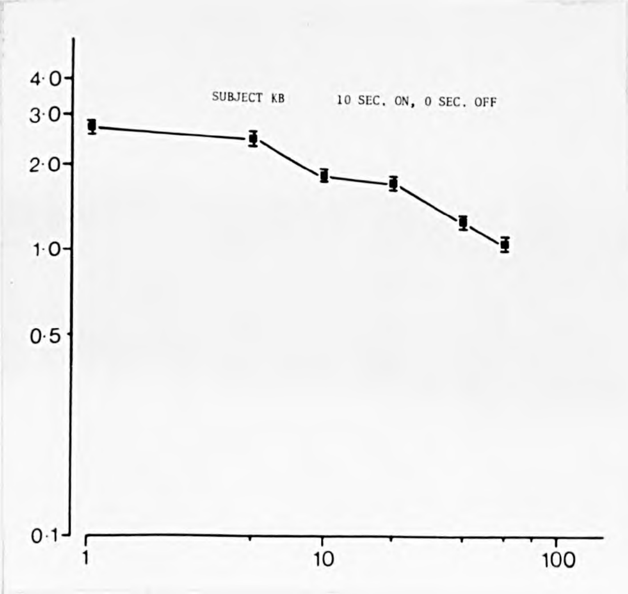


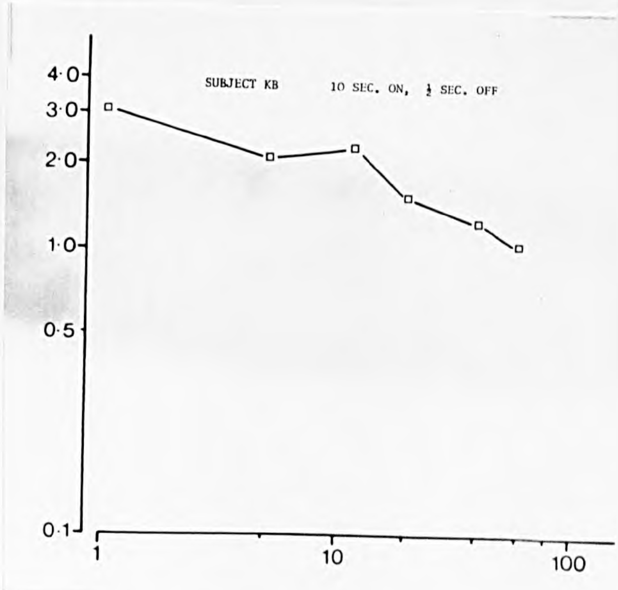


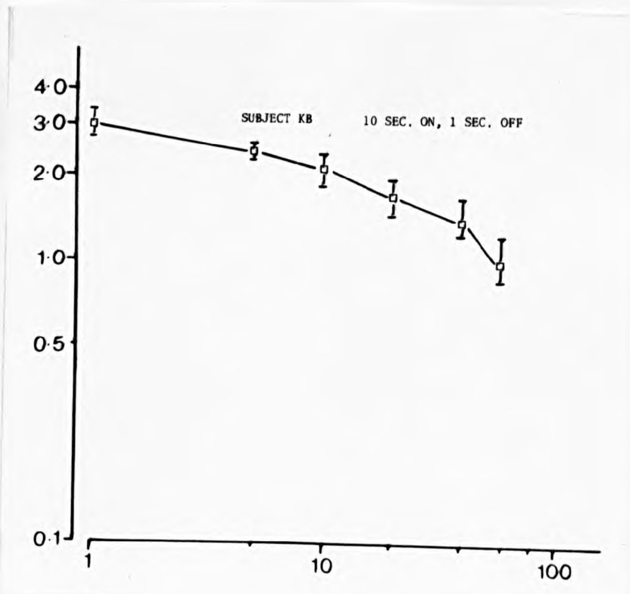
EXPERIMENTS WITH A 9 SEC. 'ON' PERIOD

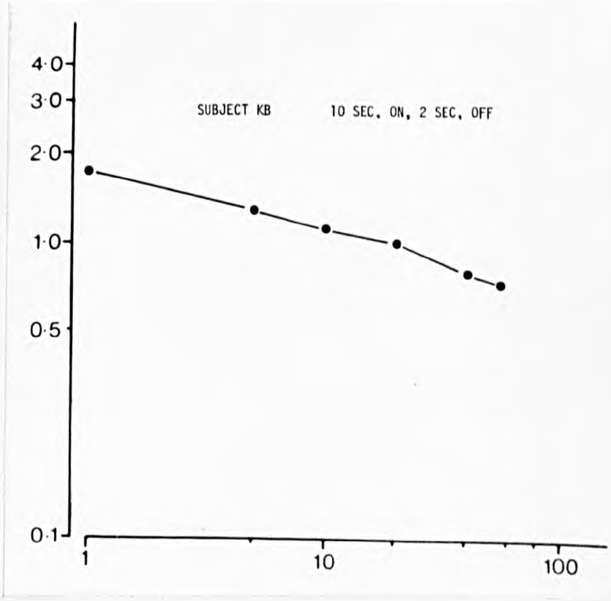


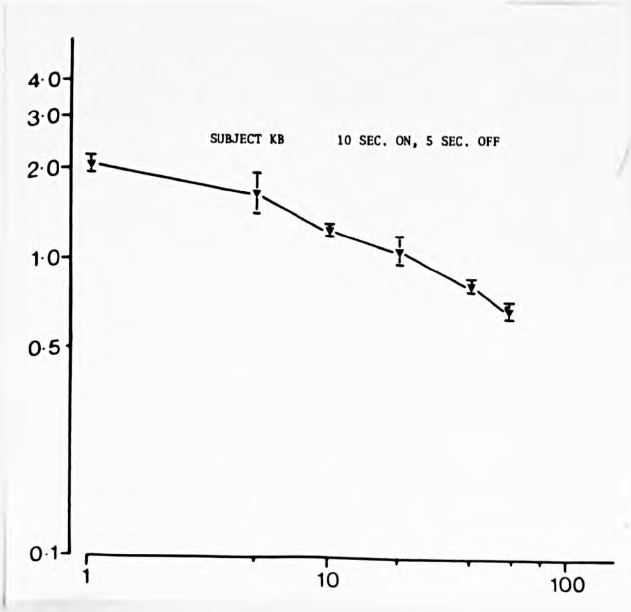
EXPERIMENTS WITH A 10 SEC. 'ON' PERIOD

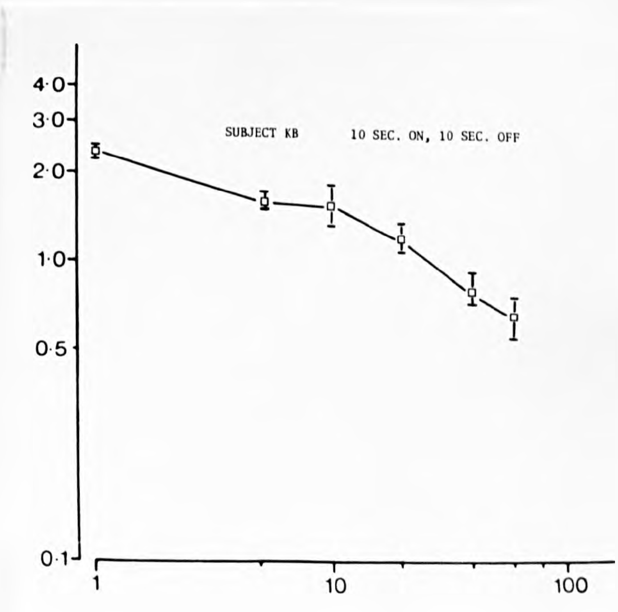




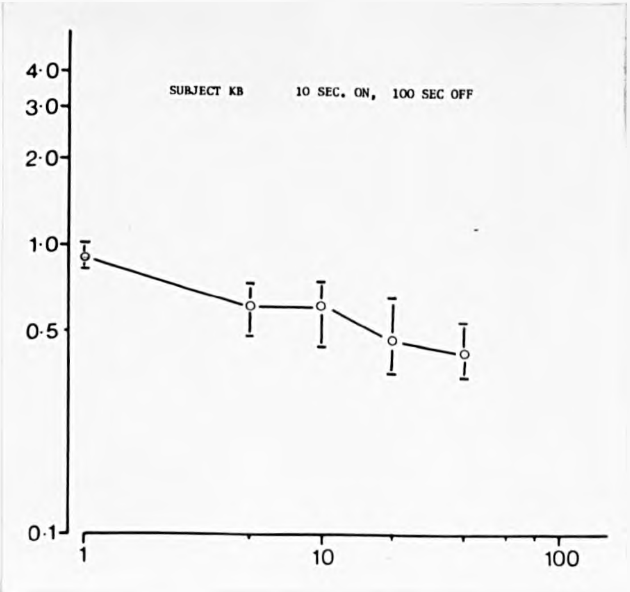


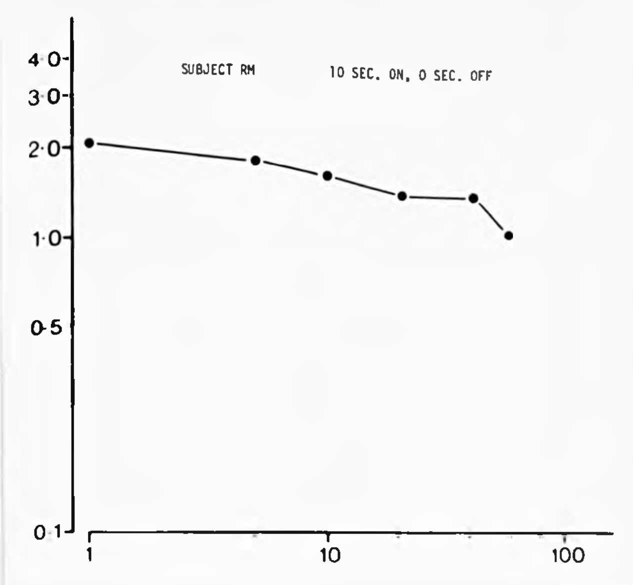


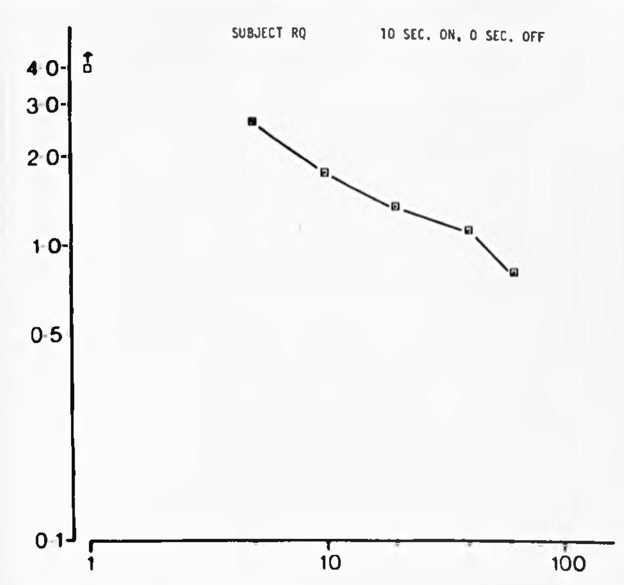


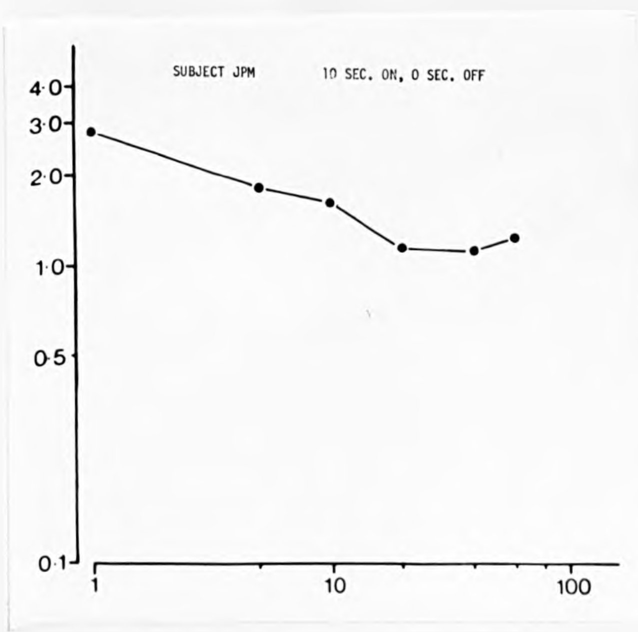


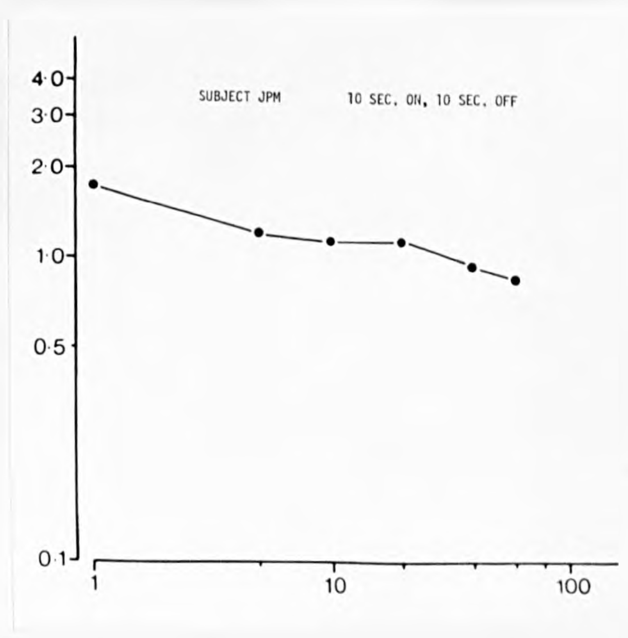
EXPERIMENTS WITH A 10 SEC. 'ON' PERIOD



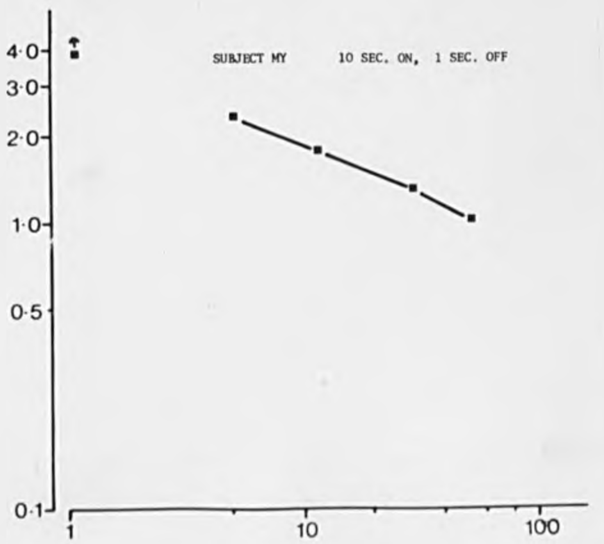


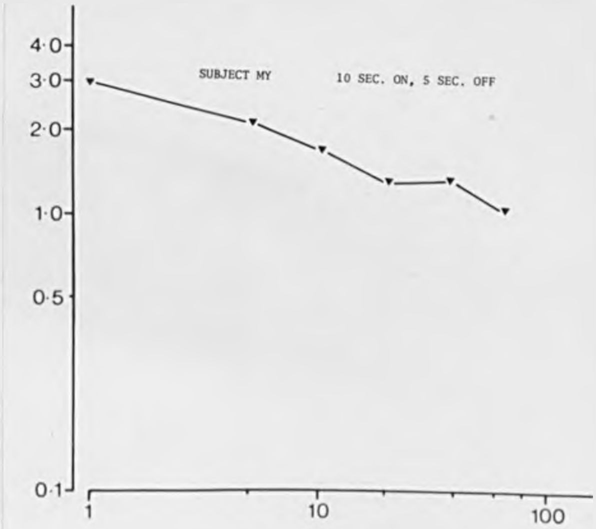


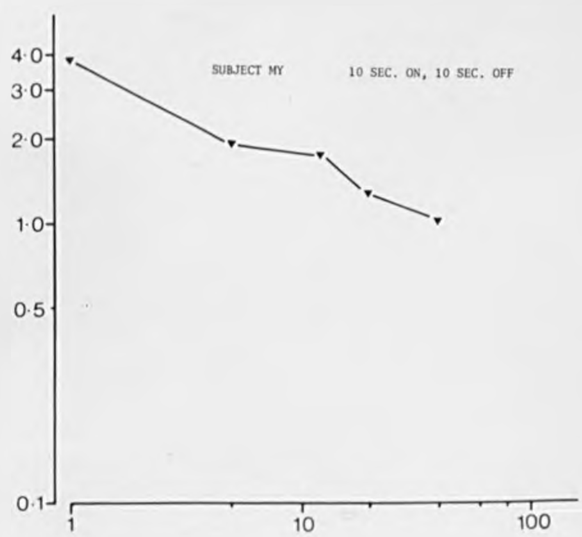


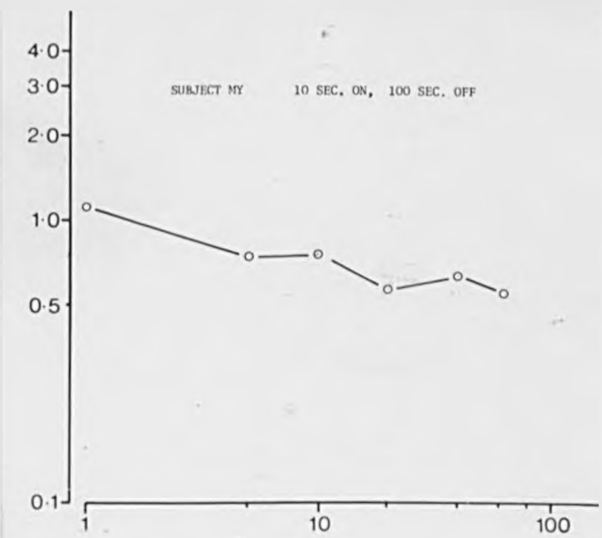


EXPERIMENTS WITH A 10 SEC. 'ON' PERIOD

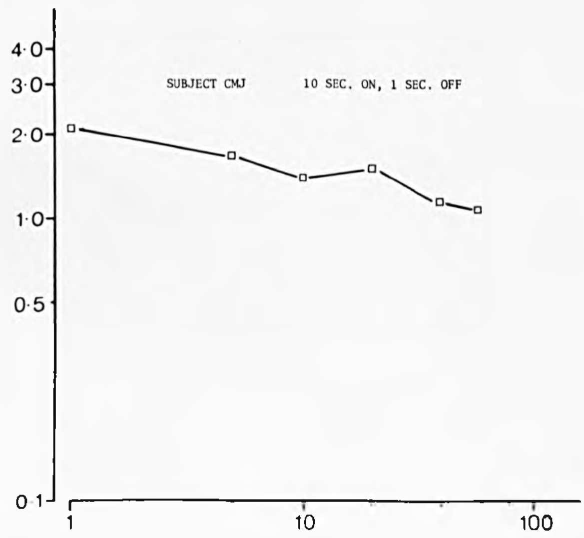


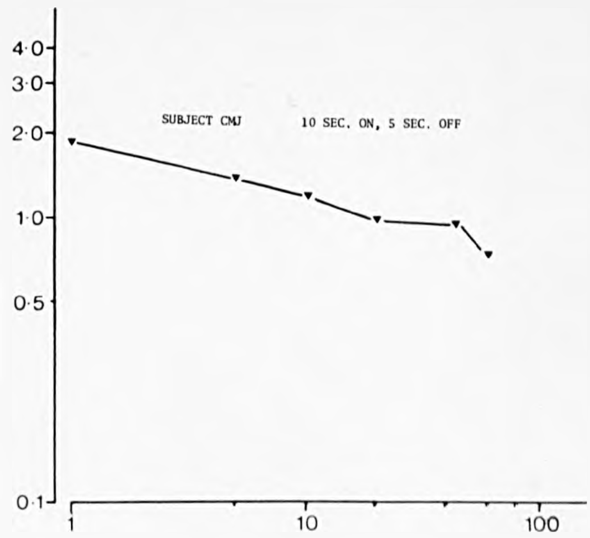


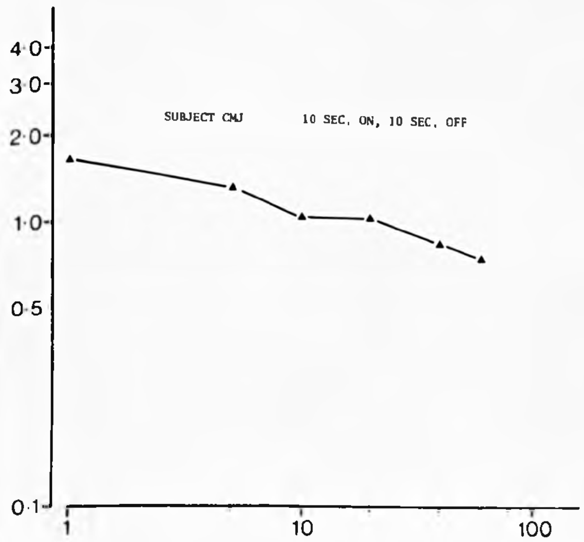


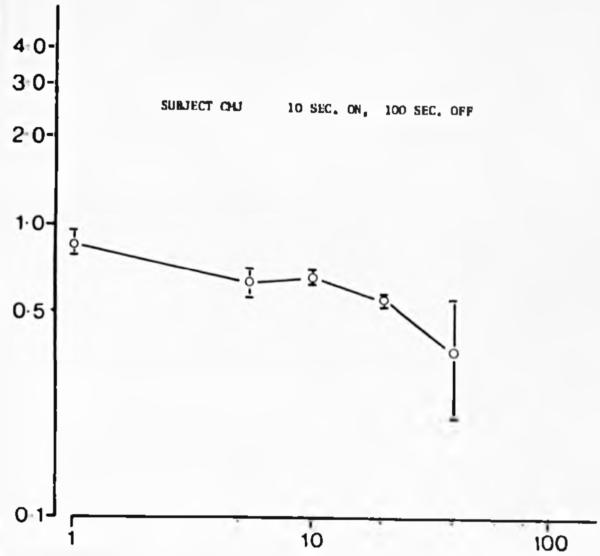


EXPERIMENTS WITH A 10 SEC. 'ON' PERIOD

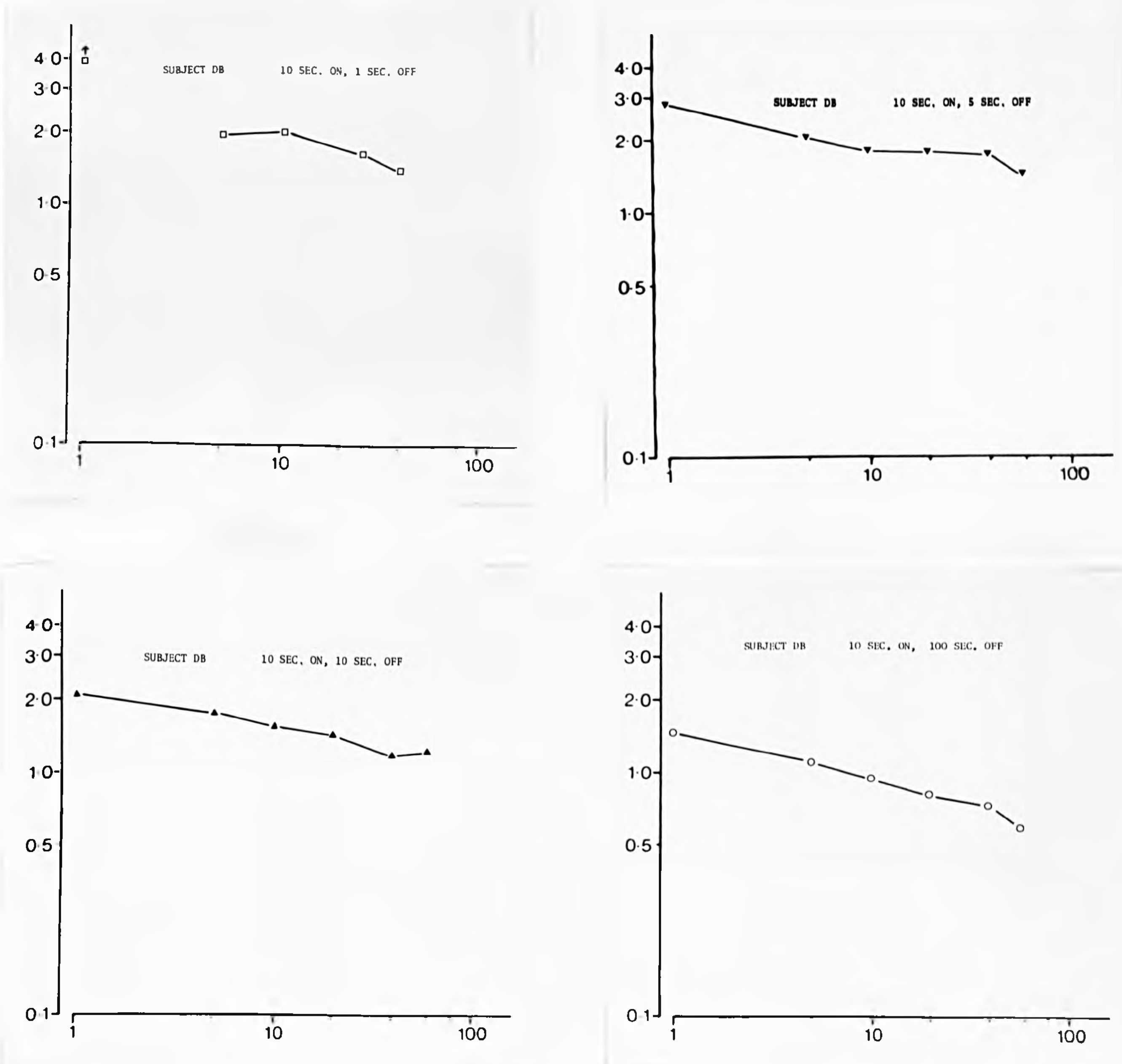




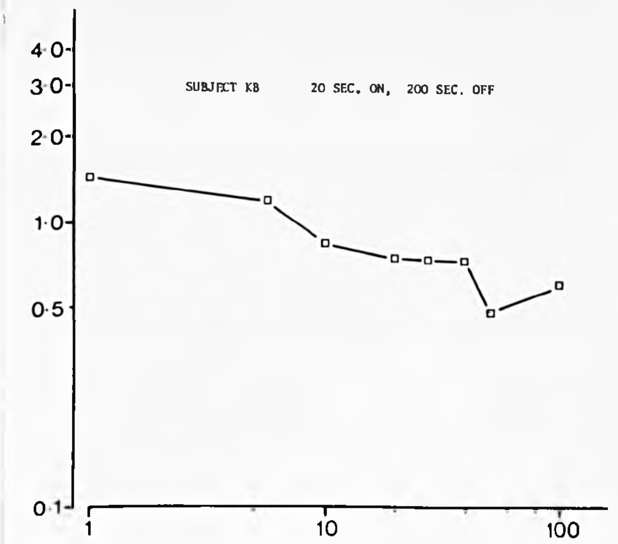




EXPERIMENTS WITH A 10 SEC. 'ON' PERIOD



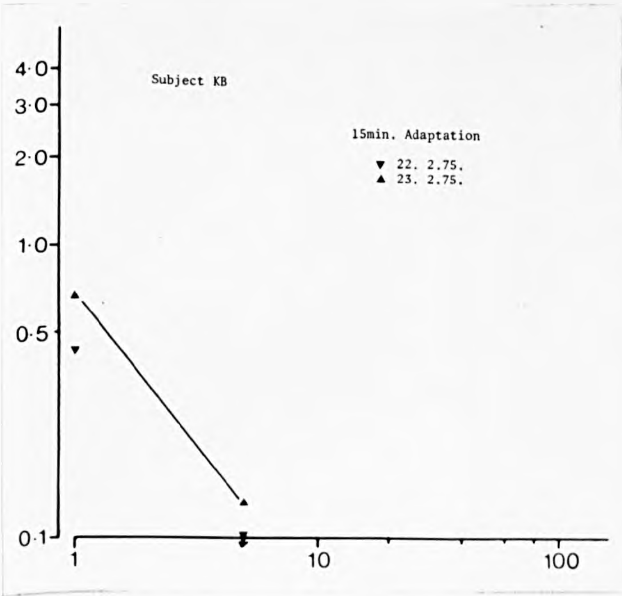
EXPERIMENTS WITH A 20 SEC. 'ON' PERIOD

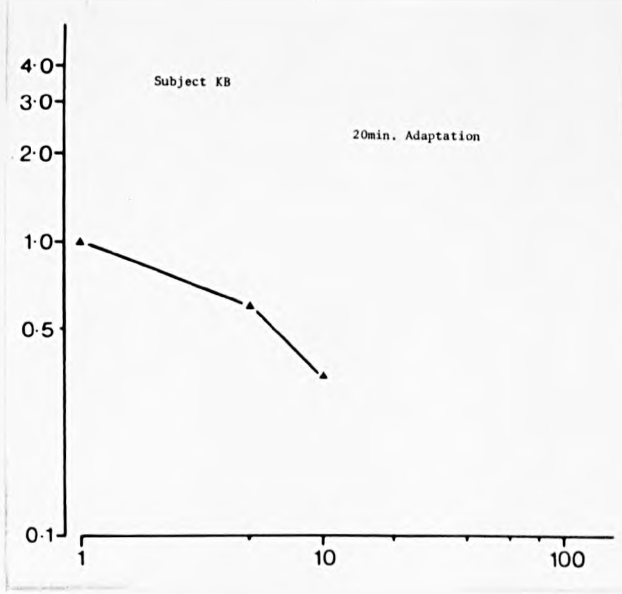


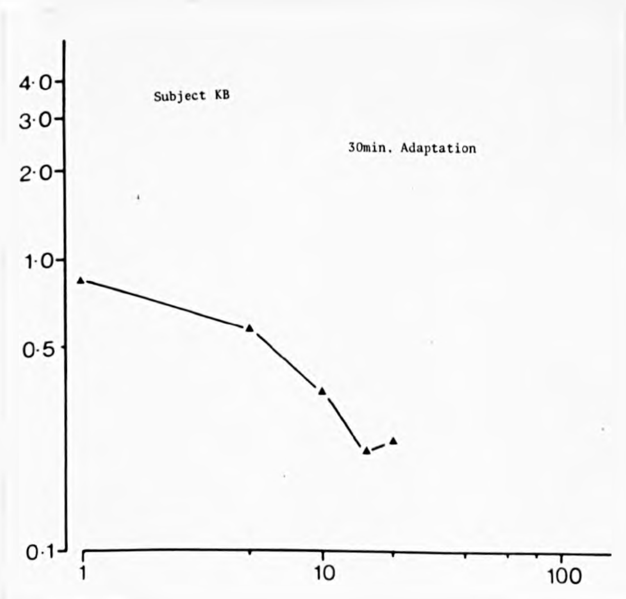
APPENDIX H:

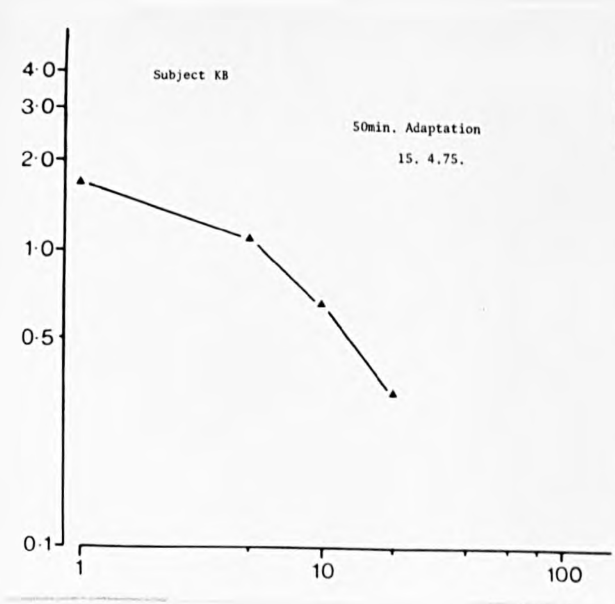
In all figures, the Y axis is the strength of the aftereffect (log. scale), and the X axis is the time, in seconds, since the end of adaptation (log. scale).

TEMPORAL SEQUENCE: ½ SEC. ON/5 SEC. OFF

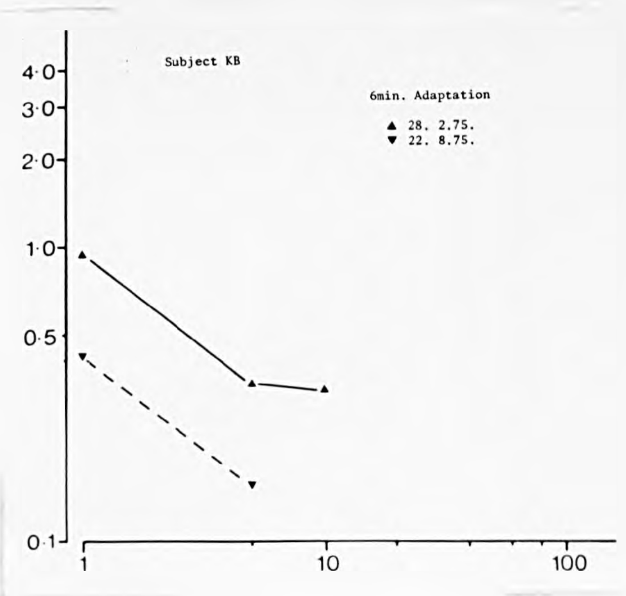


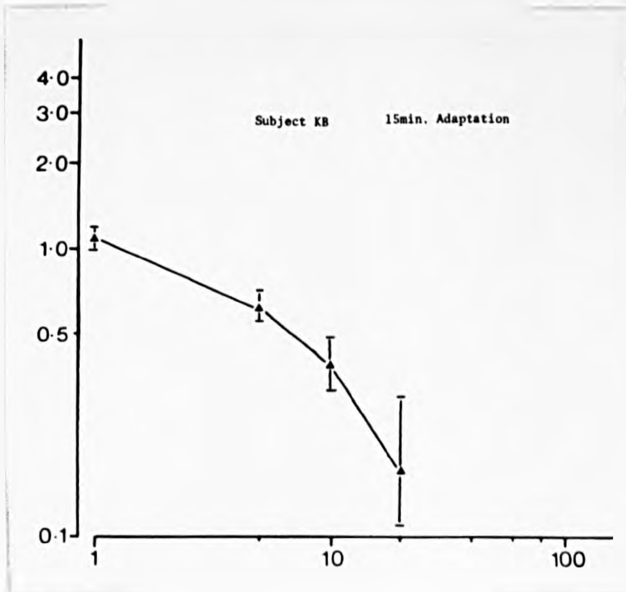


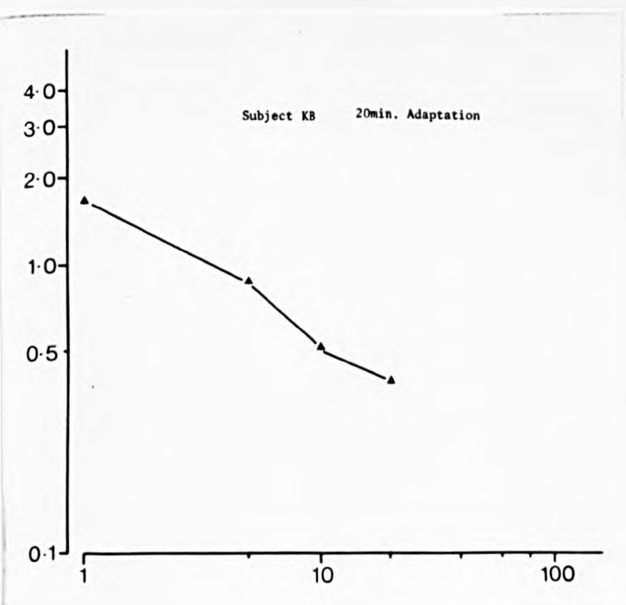


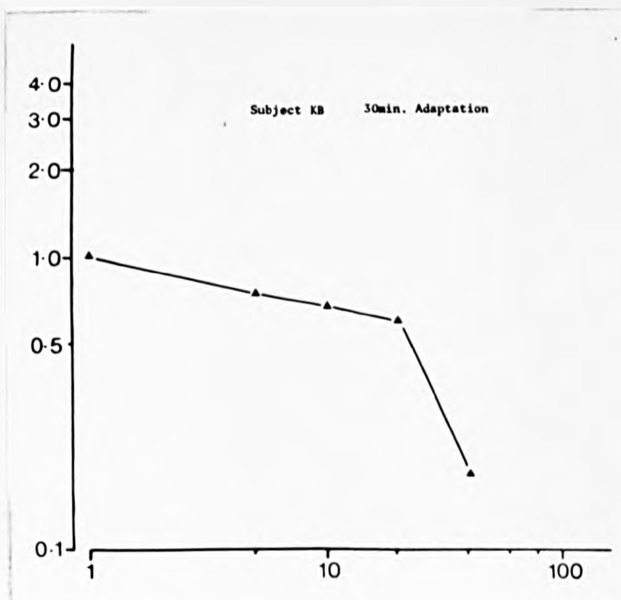


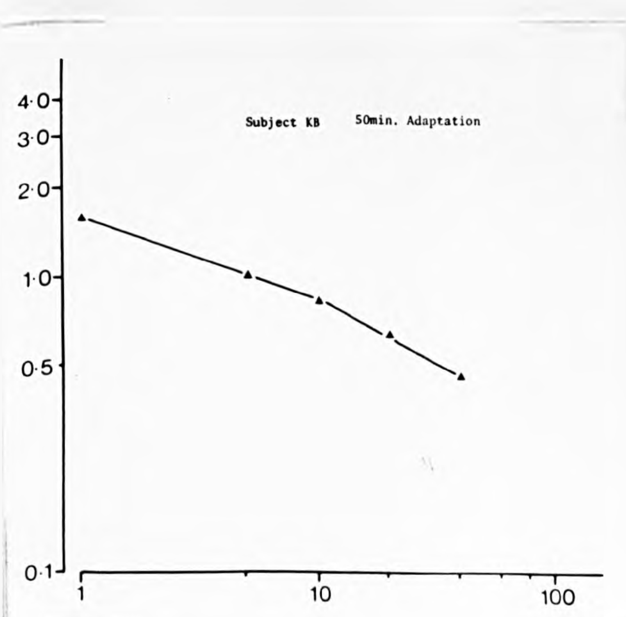
TEMPORAL SEQUENCE: 1 SEC. ON/10 SEC. OFF



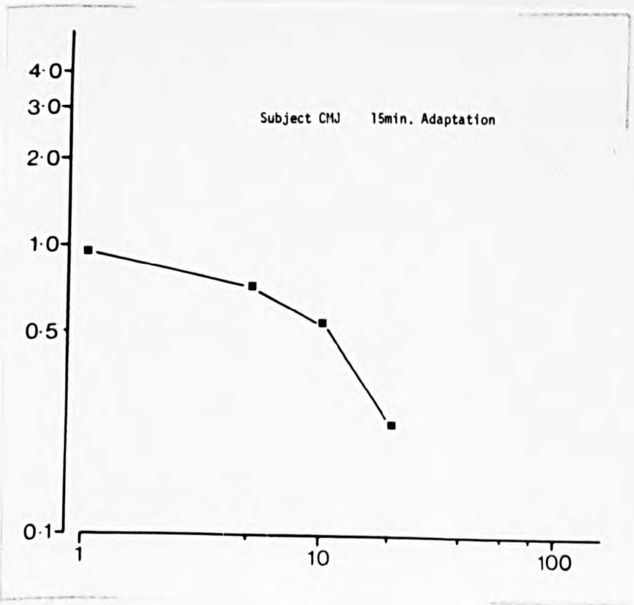


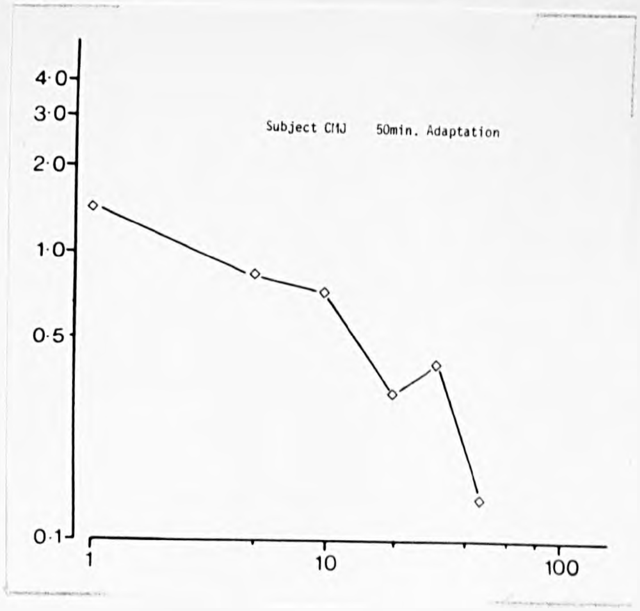


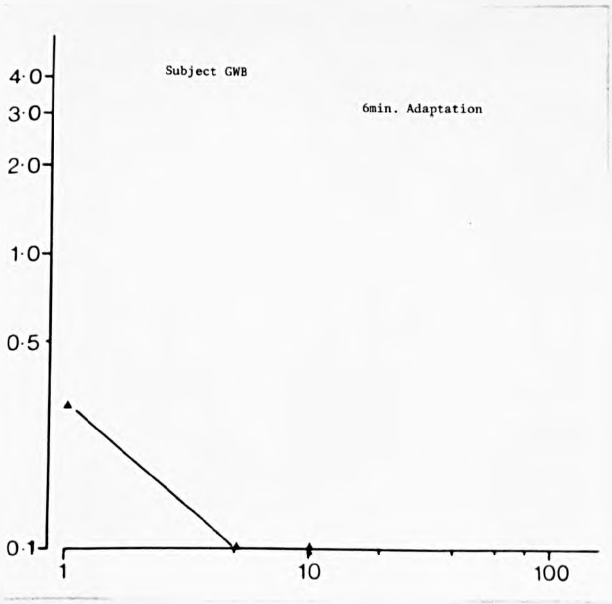


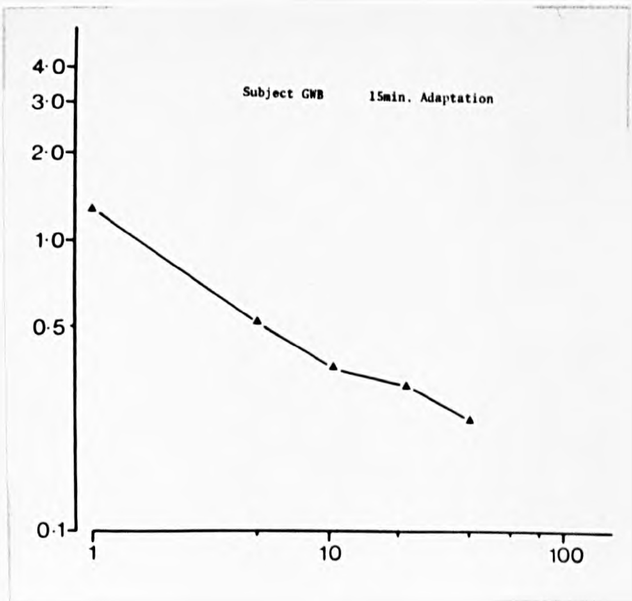


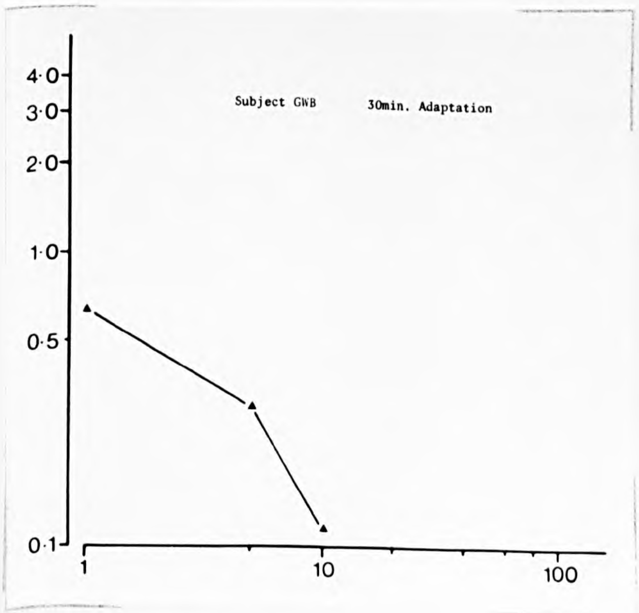
TEMPORAL SEQUENCE: 1 SEC. ON/10 SEC. OFF

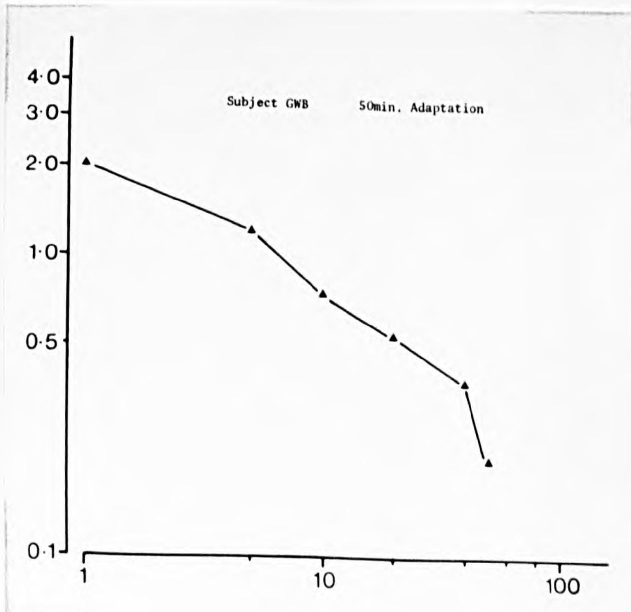




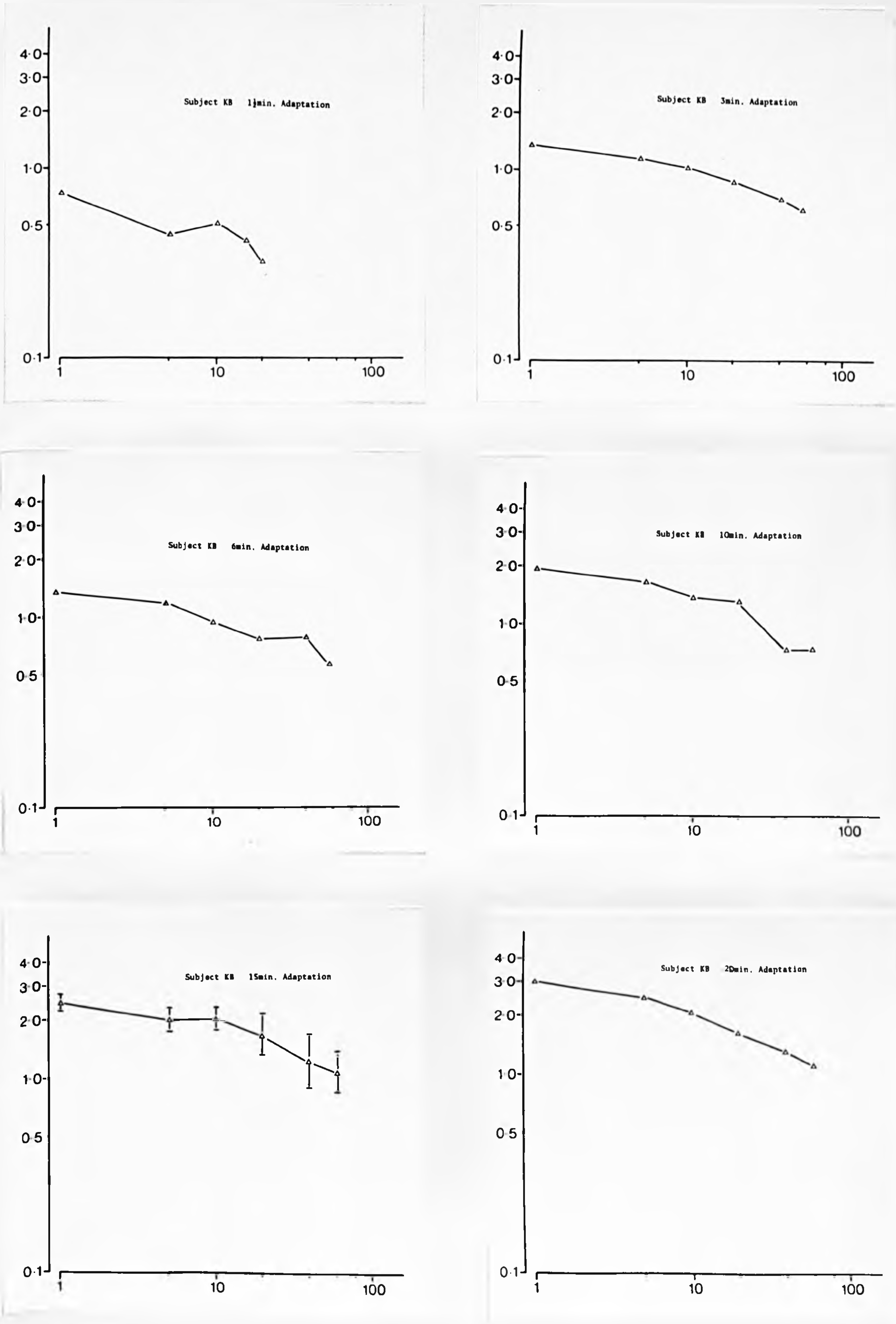




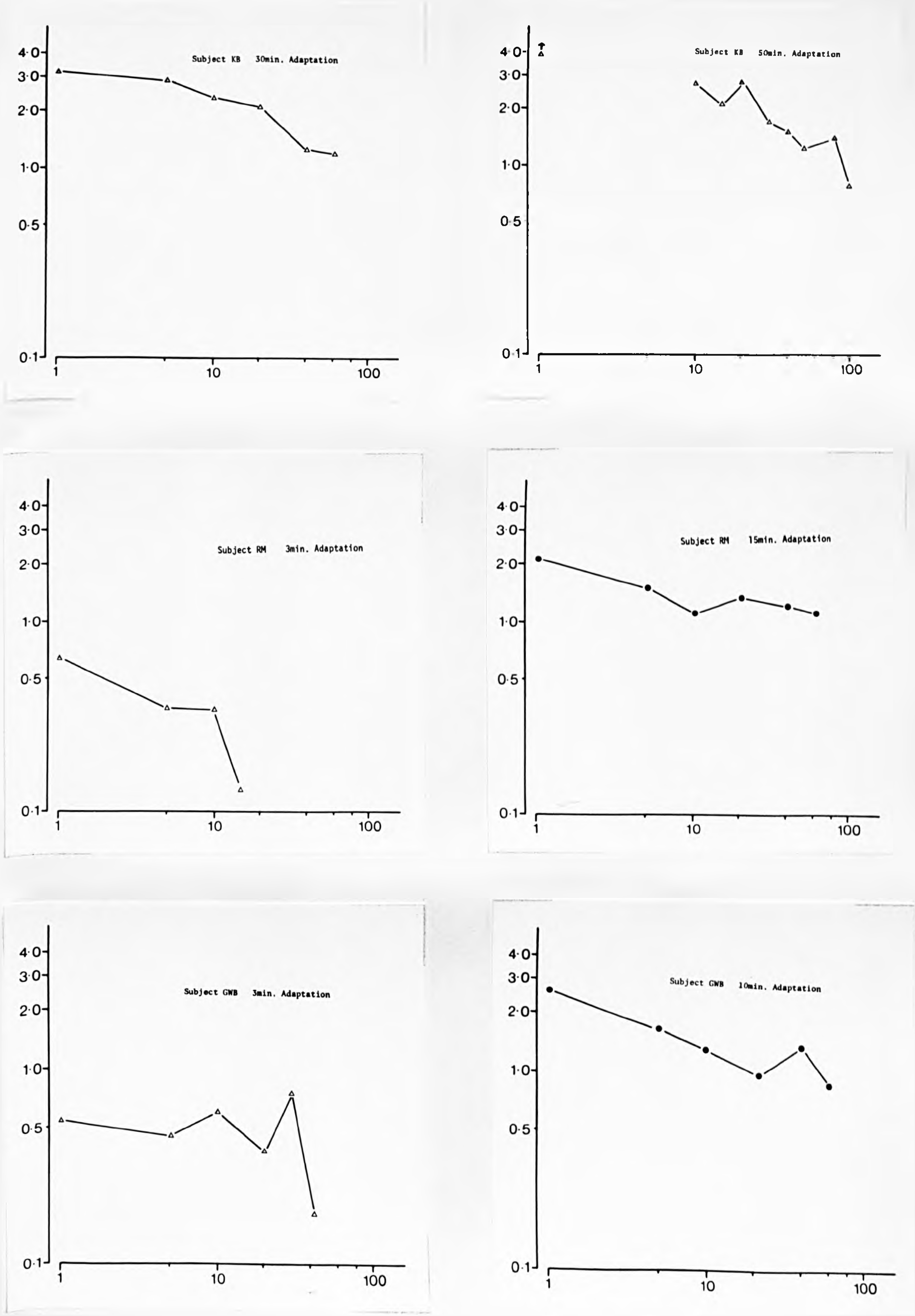




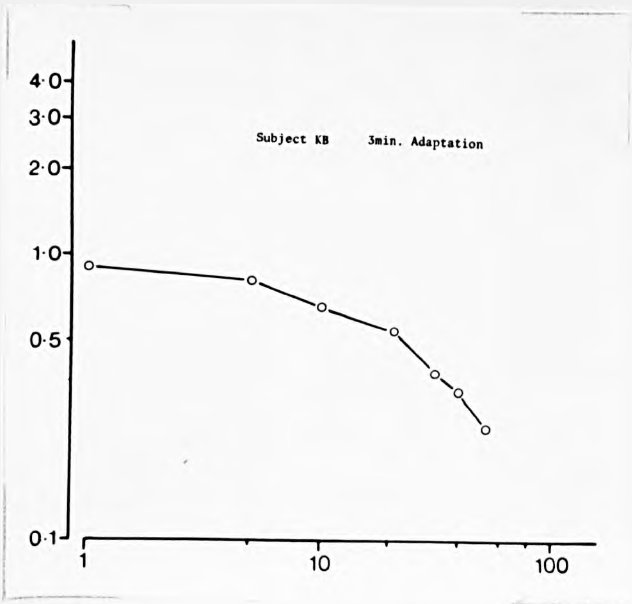
TEMPORAL SEQUENCE: 5 SEC. ON/0 SEC. OFF

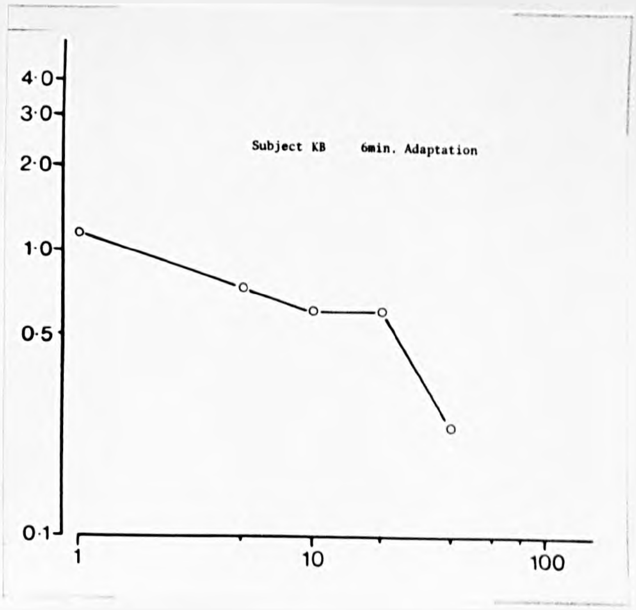


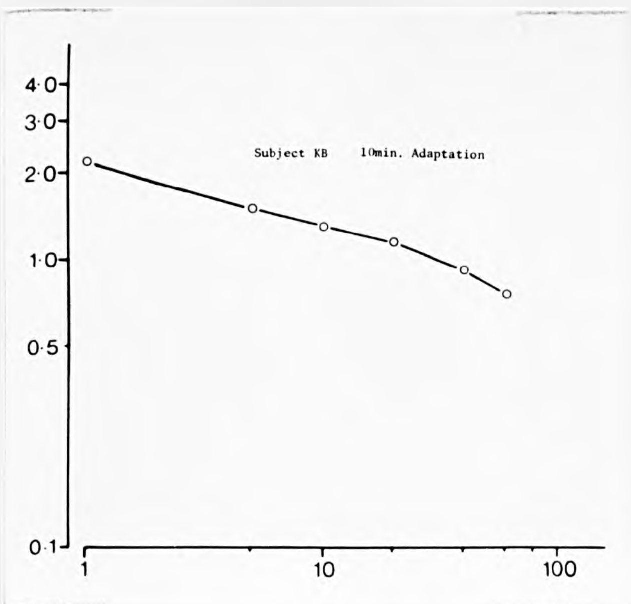
TEMPORAL SEQUENCE: 5 SEC. ON/0 SEC. OFF

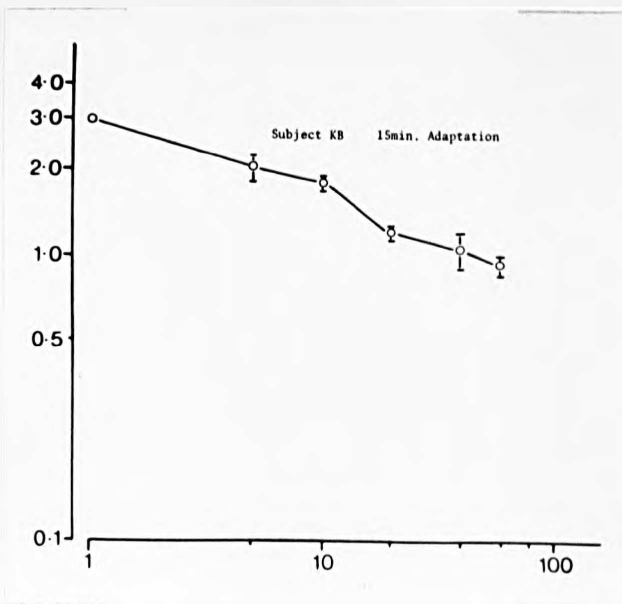


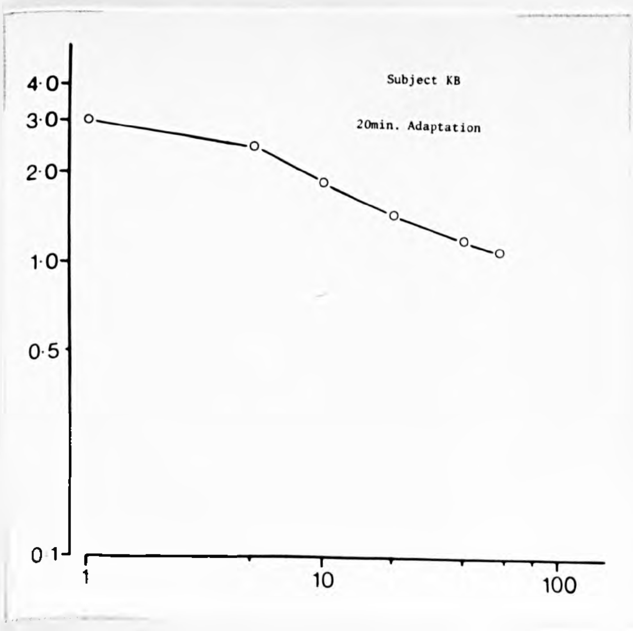
TEMPORAL SEQUENCE: 5 SEC. ON/½ SEC. OFF

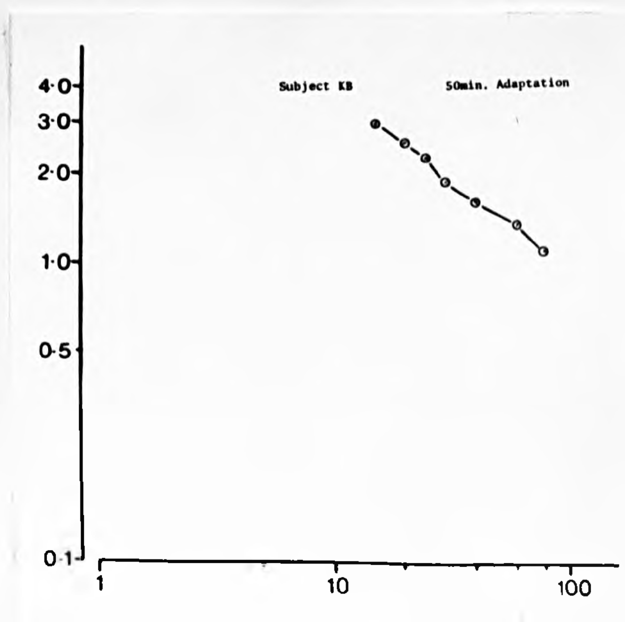




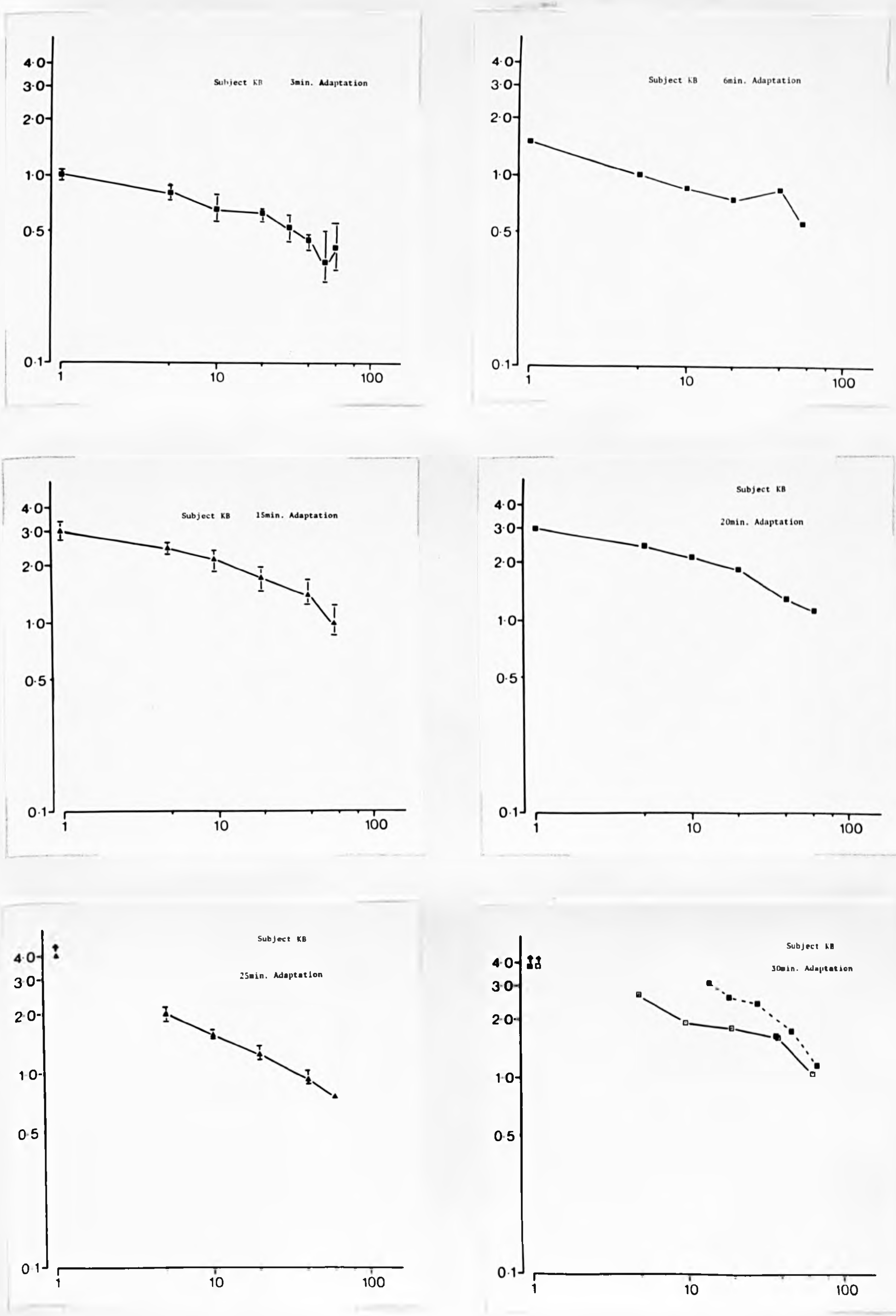




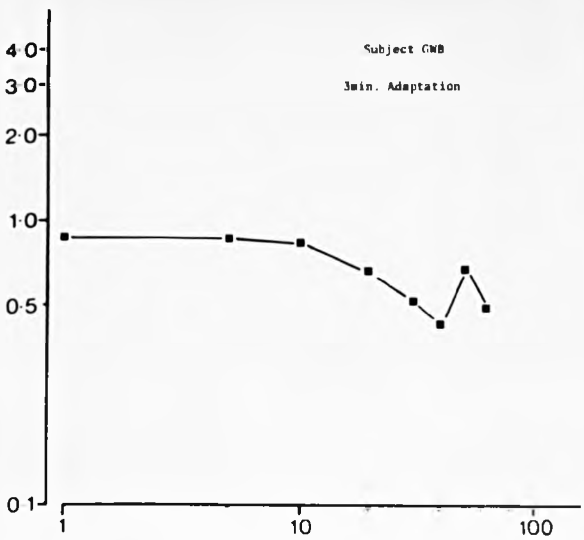


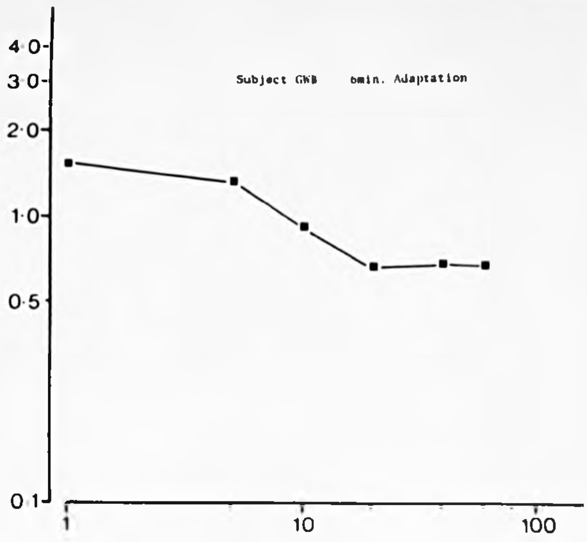


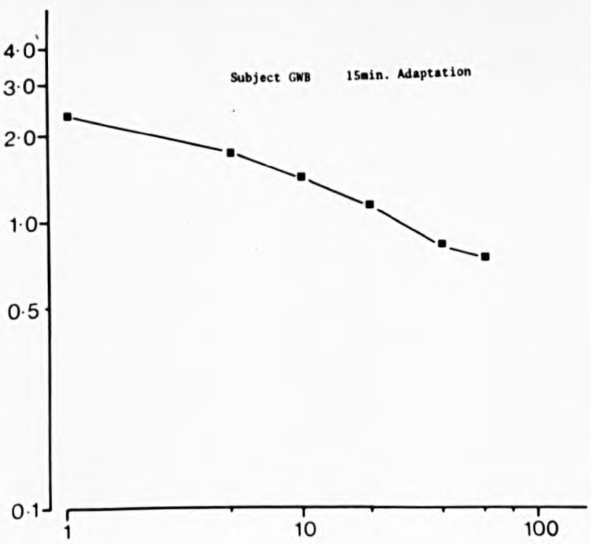
TEMPORAL SEQUENCE: 10 SEC. ON/1 SEC. OFF

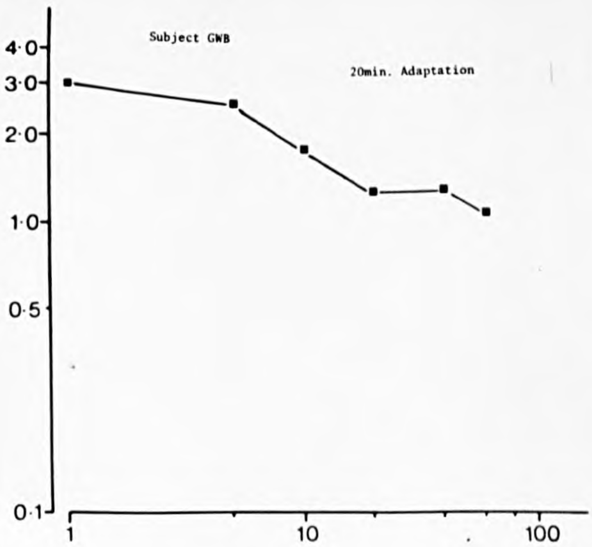


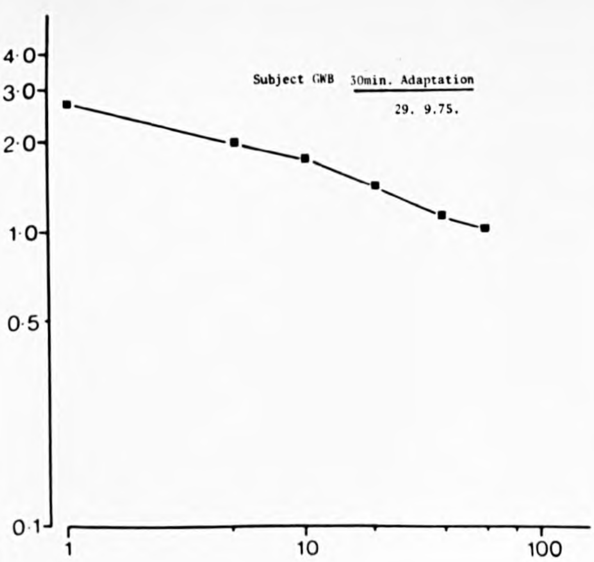
TEMPORAL SEQUENCE: 10 SEC. ON/1 SEC. OFF

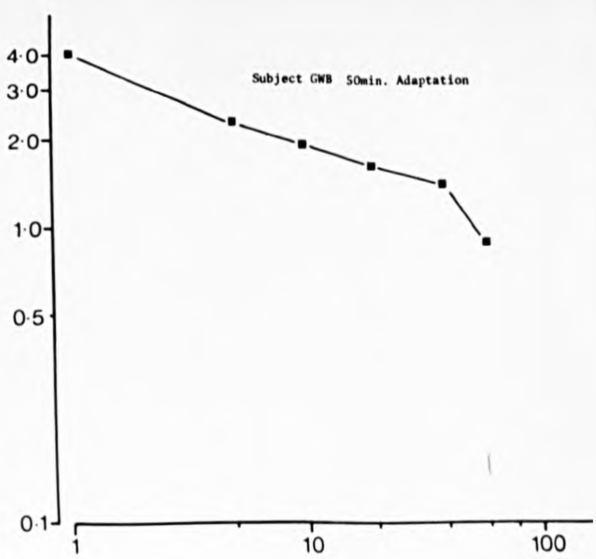




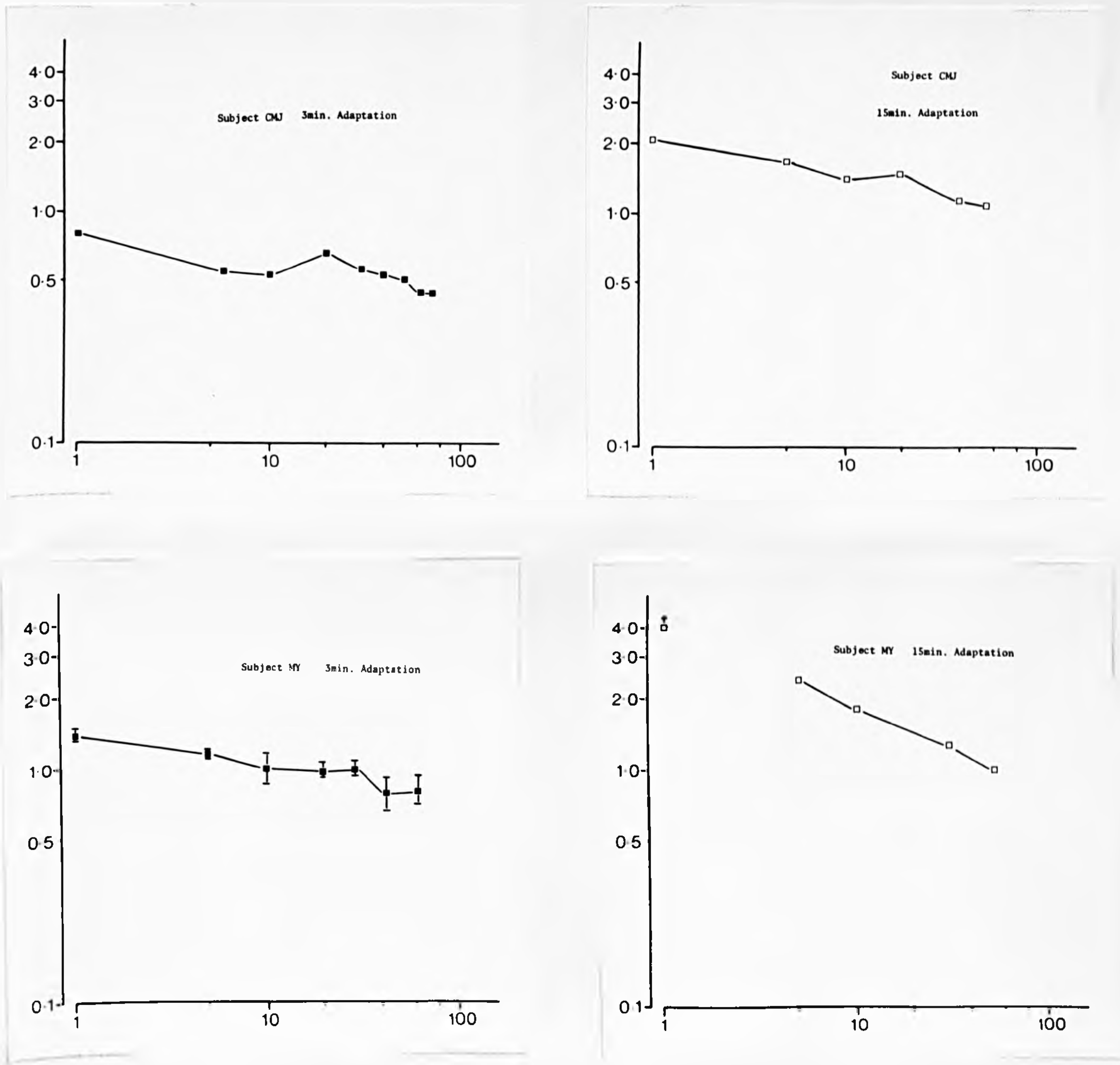




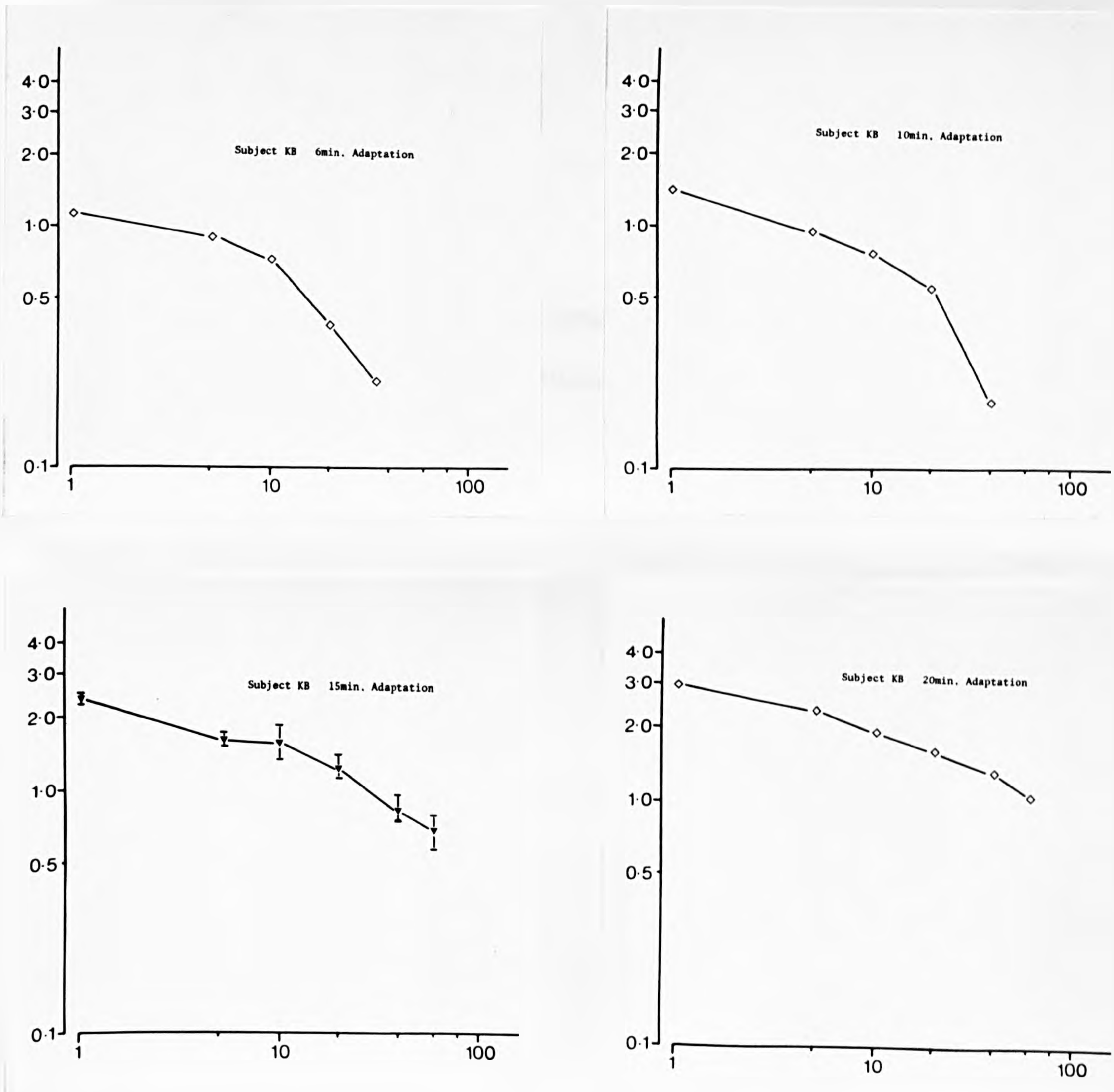




TEMPORAL SEQUENCE: 10 SEC. ON/1 SEC. OFF

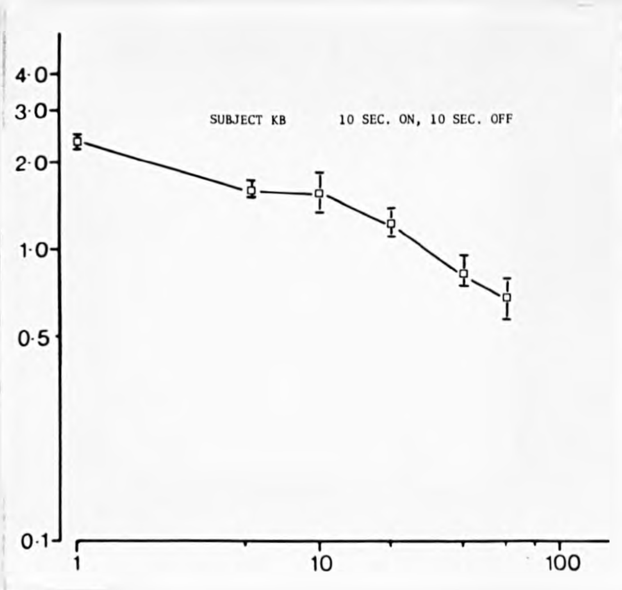


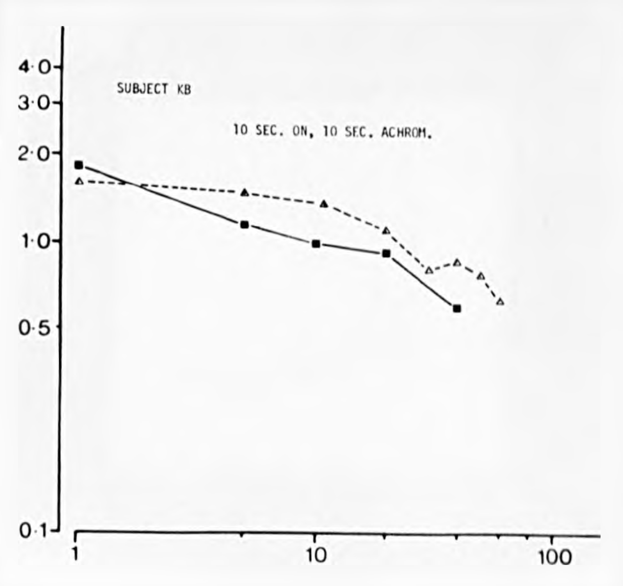
TEMPORAL SEQUENCE: 10 SEC. ON/10 SEC. OFF

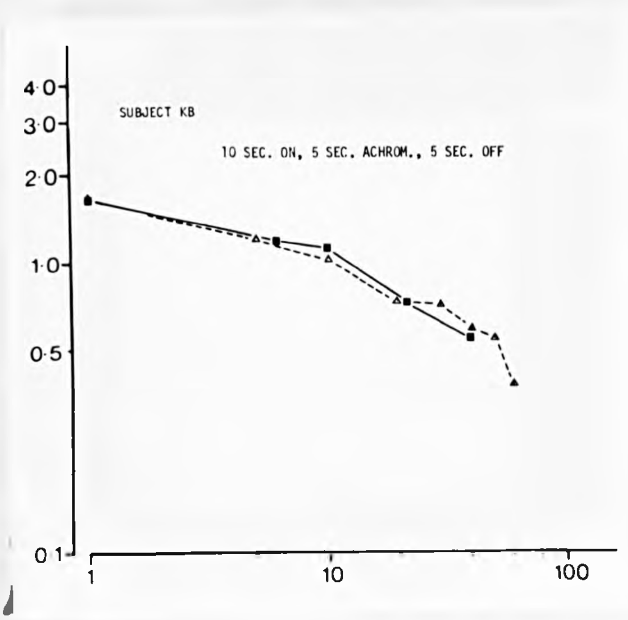


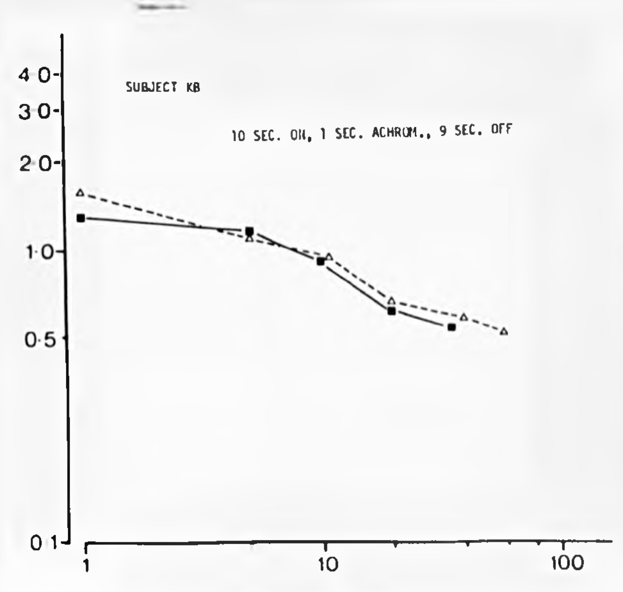
APPENDIX I:

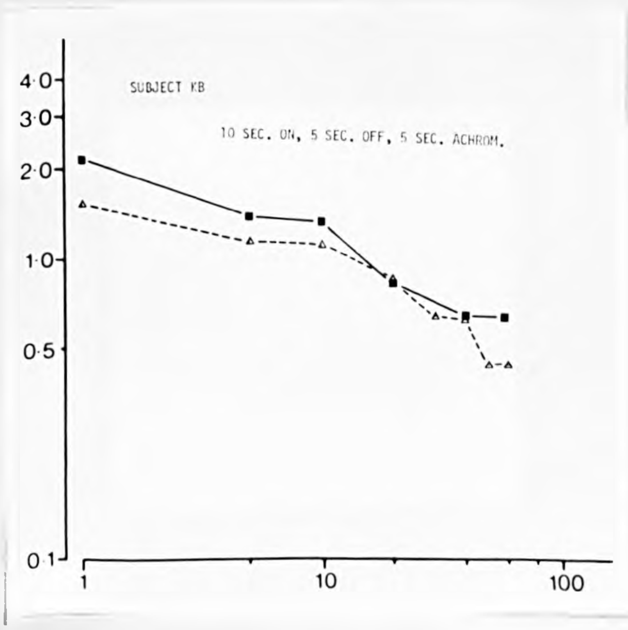
In all figures, the Y axis is the strength of the aftereffect (log. scale), and the X axis is the time, in seconds, since the end of adaptation (log. scale).

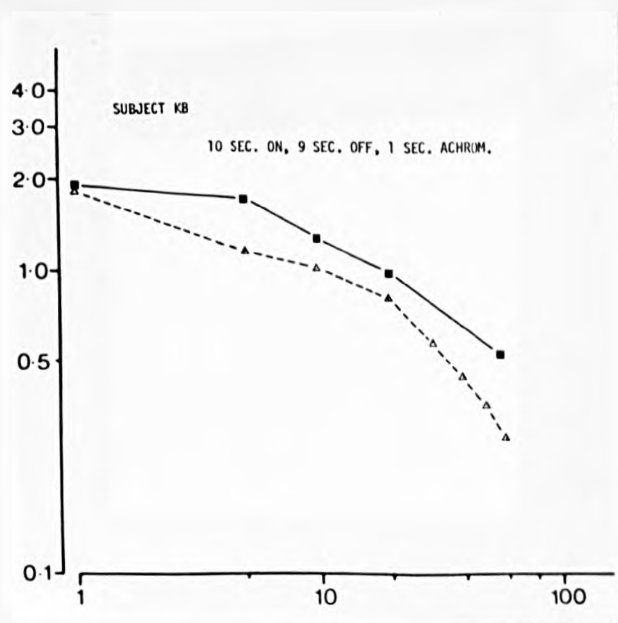

SUBJECT KB
10 SEC. ON, 10 SEC. OFF
4·0
3·0
2·0
1·0
0·5
0·1
1
10
100

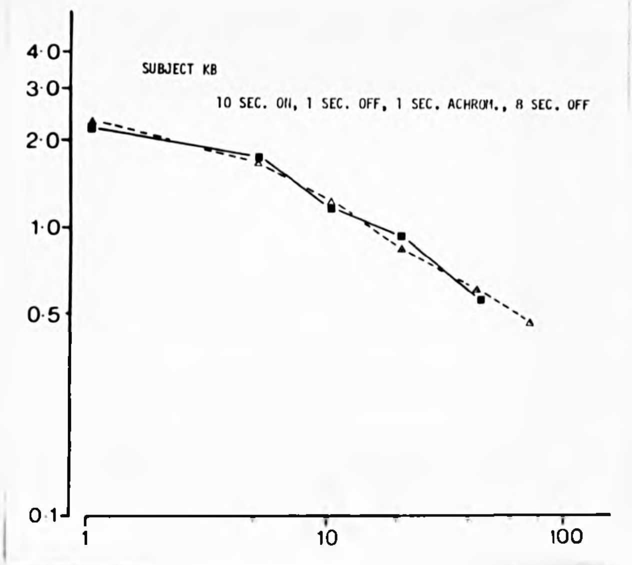

SUBJECT KB
10 SEC. ON, 10 SEC. ACHROM.
4·0
3·0
2·0
1·0
0·5
0·1
1
10
100

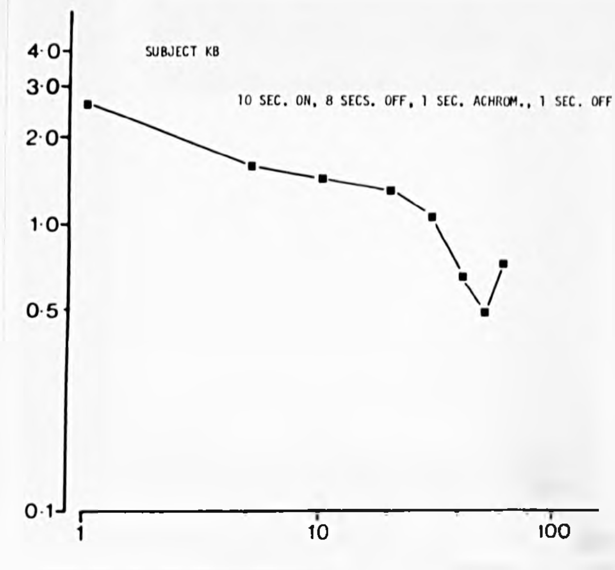

SUBJECT KB
10 SEC. ON, 5 SEC. ACHROM., 5 SEC. OFF
4·0
3·0
2·0
1·0
0·5
0·1
1
10
100

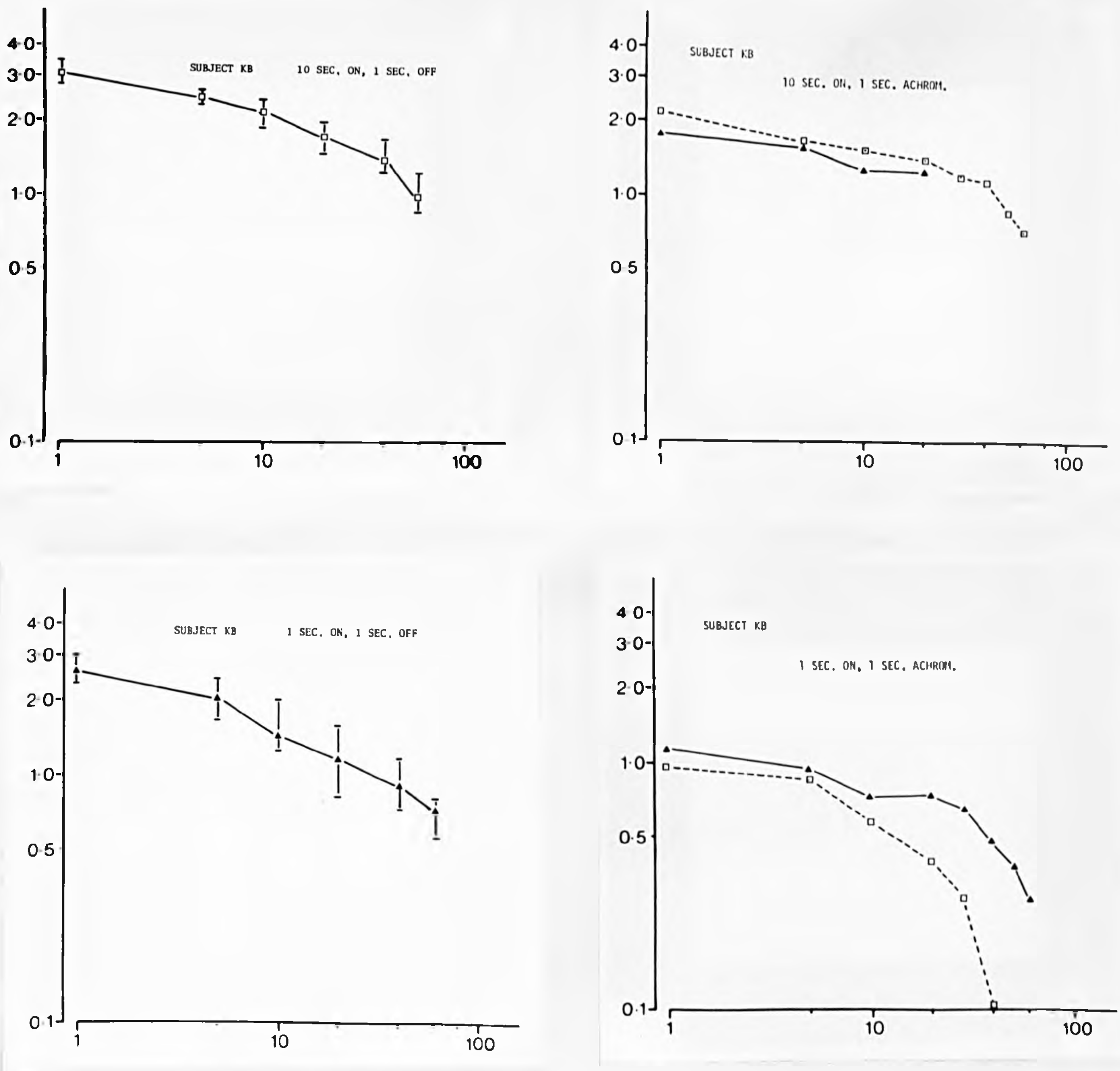

SUBJECT KB
10 SEC. ON, 1 SEC. ACHROM., 9 SEC. OFF
4·0
3·0
2·0
1·0
0·5
0·1
1
10
100


SUBJECT KB
10 SEC. ON, 5 SEC. OFF, 5 SEC. ACHROM.
4·0
3·0
2·0
1·0
0·5
0·1
1
10
100

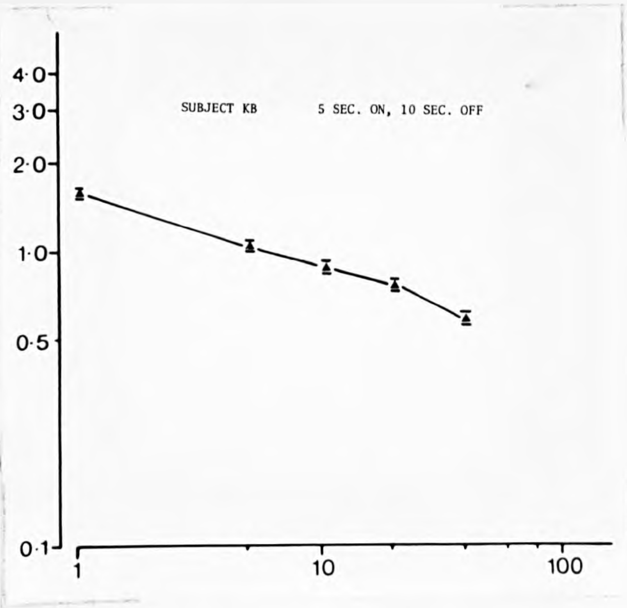

SUBJECT KB
10 SEC. ON, 9 SEC. OFF, 1 SEC. ACHROM.
4·0
3·0
2·0
1·0
0·5
0·1
1
10
100

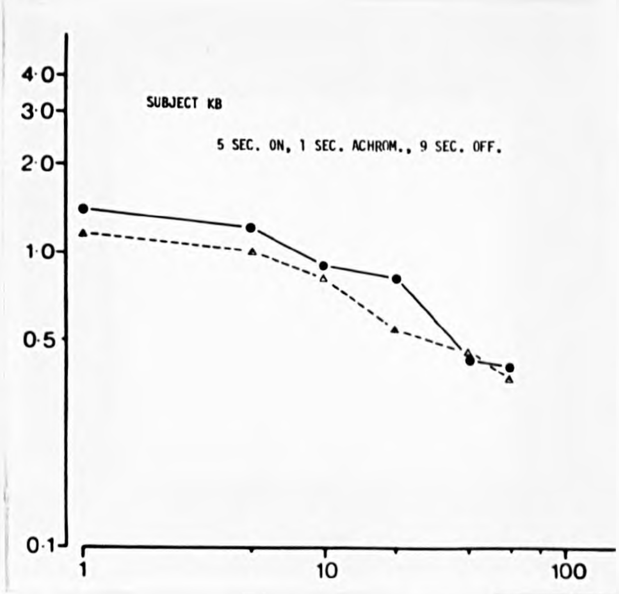

SUBJECT KB
10 SEC. ON, 1 SEC. OFF, 1 SEC. ACHROM., 8 SEC. OFF
4·0
3·0
2·0
1·0
0·5
0·1
1
10
100

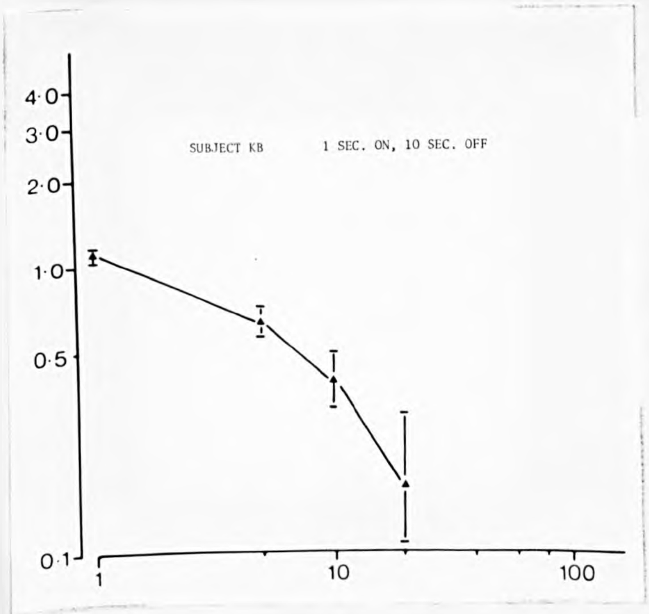

SUBJECT KB
10 SEC. ON, 8 SECS. OFF, 1 SEC. ACHROM., 1 SEC. OFF
4·0
3·0
2·0
1·0
0·5
0·1
1
10
100

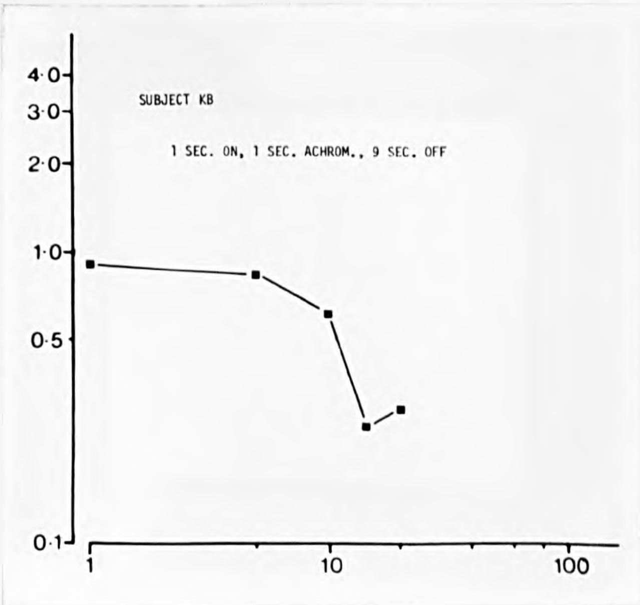


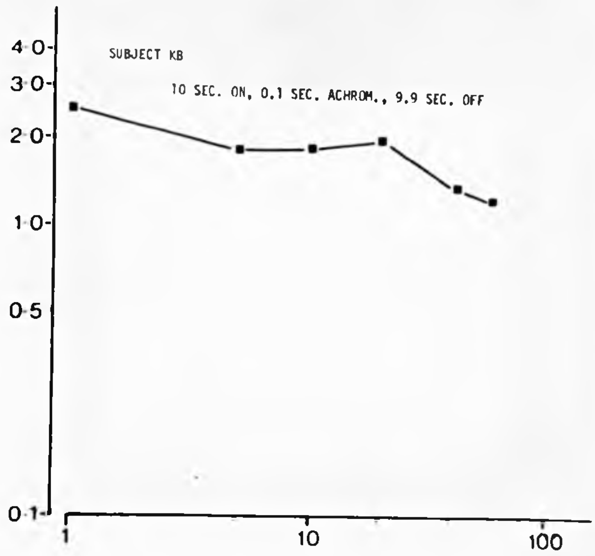
SUBJECT KB
10 SEC. ON, 1 SEC. OFF
4·0
3·0
2·0
1·0
0·5
0·1
1
10
100
SUBJECT KB
10 SEC. ON, 1 SEC. ACHROM.
4·0
3·0
2·0
1·0
0·5
0·1
1
10
100
SUBJECT KB
1 SEC. ON, 1 SEC. OFF
4·0
3·0
2·0
1·0
0·5
0·1
1
10
100
SUBJECT KB
1 SEC. ON, 1 SEC. ACHROM.
4·0
3·0
2·0
1·0
0·5
0·1
1
10
100

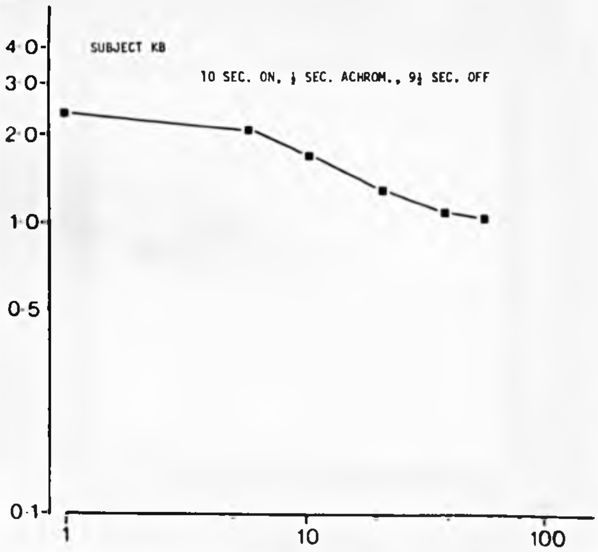

4·0
3·0
2·0
1·0
0·5
0·1
SUBJECT KB
5 SEC. ON, 10 SEC. OFF
1
10
100

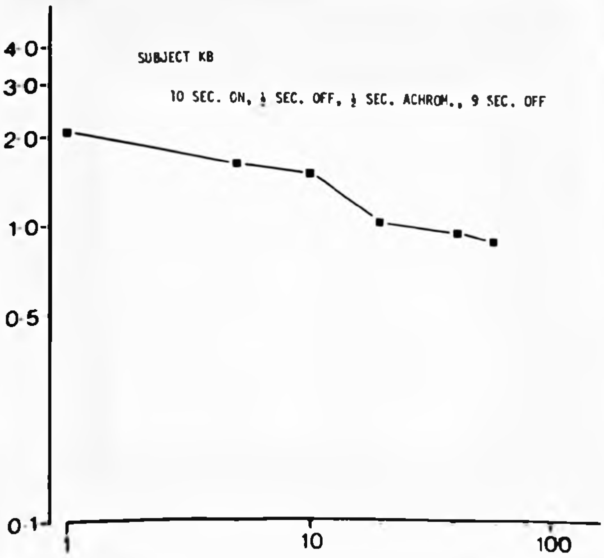

4·0
3·0
2·0
1·0
0·5
0·1
SUBJECT KB
5 SEC. ON, 1 SEC. ACHROM., 9 SEC. OFF.
1
10
100


4·0
3·0
2·0
1·0
0·5
0·1
SUBJECT KB
1 SEC. ON, 10 SEC. OFF
1
10
100


4·0
3·0
2·0
1·0
0·5
0·1
SUBJECT KB
1 SEC. ON, 1 SEC. ACHROM., 9 SEC. OFF
1
10
100


SUBJECT KB
10 SEC. ON, 0.1 SEC. ACHROM., 9.9 SEC. OFF
4·0
3·0
2·0
1·0
0·5
0·1
1
10
100


SUBJECT KB
10 SEC. ON, ½ SEC. ACHROM., 9½ SEC. OFF
4·0
3·0
2·0
1·0
0·5
0·1
1
10
100


SUBJECT KB
10 SEC. ON, ½ SEC. OFF, ½ SEC. ACHROM., 9 SEC. OFF
4·0
3·0
2·0
1·0
0·5
0·1
1
10
100

REFERENCES

Andrews, D.P. (1965). Perception of contours in the central fovea. Nature, 205, 1218-1220.

Andrews, D.P. (1972). The site of the adaptation shown in figural after-effects. Vision Research, 12, 1065-1067.

Attneave, F. (1954). Some informational aspects of visual perception. Psychological Review, 16, 183-193.

Barlow, H.B. (1963). Possible principles underlying the transformations of sensory messages. In: Sensory Communication (ed. W. Rosenblith), M.I.T. Press.

Barlow, H.B. and G.S. Brindley, (1963). Inter-ocular transfer of movement after-effects during pressure blinding of the stimulated eye. Nature, 200, 1347.

Barlow, H.B. and R.M. Hill (1963). Evidence for a physiological explanation of the waterfall phenomenon and figural after-effects. Nature, 200, 1345-1347.

Benevento, L.A., O.D. Creutzfeldt and U. Kuhnt (1972). Significance of intracortical inhibition in the visual cortex. Nature: New Biology. 238, 124-126.

Bishop, P.O. and G.H. Henry (1972). Striate neurones: receptive field concepts. Investigative Ophthalmology, 11, 346-354.

Blake, R. and R. Fox (1972). Interocular transfer of adaptation to spatial frequency during retinal ischaemia. Nature: New Biology, 240, 76-77.

Blakemore, C. and F.W. Campbell (1969). On the existence of neurones in the human visual system selectively sensitive to the orientation and size of retinal images. Journal of Physiology, 203, 237-260.

Blakemore, C. and F.W. Campbell (1969). Adaptation to spatial stimuli. Journal of Physiology, 200, 11-13P.

Blakemore, C. and P. Sutton (1969). Size adaptation: a new aftereffect. Science, 166, 245-247.

Blakemore, C., R.H.S. Carpenter and M.A. Georgeson (1970). Lateral inhibition between orientation detectors in the human visual system. Nature, 228, 37-39.

Blakemore, C. T. Nachmias and P. Sutton (1970). The perceived spatial frequency shift: evidence for frequency-selective neurones in the human visual system. Journal of Physiology, 210, 727-750.

Boles, J. (1971). Colour and contour detection by cells representing the fovea in monkey striate cortex. Society for Neurosciences. 1st Annual Meeting.

Breitmeyer, B.G. and L.A. Cooper (1972). Frequency-specific colour adaptation in the human visual system. Perception and Psychophysics, 11, 95-96.

British National Formulary (1957). British Medical Association and Pharmaceutical Society of Great Britain. London.

Broerse, J., R. Over and W. Lovegrove (1975). Loss of wavelength selectivity in contour masking and aftereffect following dichoptic adaptation. Perception and Psychophysics, 17, 333-336.

Brindley, G.S. (1970). Physiology of the retina and visual pathway. 2nd Edition, Edward Arnold.

Brooks, B. and R. Jung (1973). Neuronal physiology of the visual cortex. (In: Handbook of Sensory Physiology, Vol. V11/3 Pt.B Ed. R. Jung). Springer-Verlag.

Brown, D.R., M.P. Cosgrove, G.A. Kohl, D.D. Fulgham and M.S. Schmidt (1975). Stabilized images: probe analysis of pattern and colour analytic mechanisms. Vision Research 15, 209-215.

Campbell, F.W., G.F. Cooper and C. Enroth-Cugell (1969). The spatial selectivity of the visual cells of the cat. Journal of Physiology, 203, 223-235.

Campbell, F.W. and E.R. Howell (1972). Monocular alternation: a method for the investigation of pattern vision. Journal of Physiology, 225, 19P.

Campbell, F.W. and J.J. Kulikowski (1966). Orientation selectivity of the human visual system. Journal of Physiology 187, 437-445.

Campbell, F.W., J.J. Kulikowski and J. Levinson (1966). The effect of orientation on the visual resolution of gratings. Journal of Physiology, 187, 427-436.

Campbell, F.W. and L. Maffei (1971). The tilt after-effect: a fresh look. Vision Research, 11, 837-840.

Carpenter, R.H.S. and C. Blakemore (1973). Interactions between orientations in human vision. Experimental Brain Research, 18, 287-303.

Coltheart, M. (1971). Visual feature analysers and after-effects of tilt and curvature. Psychological Review, 78, 114-121.

Coltheart, M. (1973). Colour-specificity and monocularity in the visual cortex. Vision Research, 13, 2595-2598.

Cornsweet, T. (1970). Visual Perception. Academic Press.

Cosgrove, M.P., G.A. Kohl, M. Schmidt and D.R. Brown (1974). Chromatic substitution with stabilised images: evidence for chromatic-specific pattern processing in the human visual system. Vision Research, 14, 23-29.

Creutzfeldt, O.D. (1974). Some neurophysiological considerations concerning "memory". (In: Memory and Transfer of Information. Ed. H.P. Zippel, Plenum: New York).

Creutzfeldt, O.D. and P. Heggelund (1975). Neural plasticity in visual cortex of adult cats after exposure to visual patterns. Science, 188, 1025-1027.

De Valois, R.L. (1973). Central mechanisms of colour vision. (In: Handbook of Sensory Physiology, Vol. VII/3 Pt A. Ed. R. Jung, Springer-Verlag.

Dealy, R.S. and D.J. Tolhurst (1974). Is spatial adaptation an after-effect of prolonged inhibition? Journal of Physiology, 241, 261-270.

Dick, A.O. (1974). Iconic memory and its relation to perceptual processing and other memory mechanisms. Perception and Psychophysics, 16, 575-596.

Dow, B.M. and P. Gouras (1973). Color and spatial specificity of single units in rhesus monkey striate cortex. Journal of Neurophysiology, XXXVI, 79-100.

Downie, N.M. and R.W. Heath (1965). Basic Statistical Methods. 2nd Edition, Harper and Row.

Eccles, J.C. (1973). The Understanding of the Brain. McGraw-Hill.

Fidell, L.S. (1970). Orientation specificity in chromatic adaptation of "edge-detectors". Perception and Psychophysics, 8, 235-237.

Freund, H.-J. (1973). Neuronal mechanisms of the lateral Geniculate Body (In: Handbook of Sensory Physiology, Vol. VII/3 Pt B. Ed. R. Jung). Springer-Verlag.

Gibson, J.J. (1937). Adaptation with negative after-effect. Psychological Review, 44, 222-244.

Gilinski, A.S. (1968). Orientation-specific effects of patterns of adapting light on visual acuity. Journal of the Optical Society of America, 58, 13-18.

Gilinski, A.S., E.P. Boyko and H.L. Baras (1967). Resolution of lines with specific orientation after patterned-light adaptation. Journal of the Optical Society of America, 57, p581-

Gilinski, A.S. and R.S. Doherty (1969). Interocular transfer of orientation effects. Science 164, 454-455.

Gouras, P. (1972). Colour opponency from fovea to striate cortex. Investigative Ophthalmology, 11, 427-434.

Gouras, P. (1974). Opponent-colour cells in different layers of foveal striate cortex. Journal of Physiology, 238, 583-602.

Gouras, P. and J. Kruger (1975). Similarities of colour properties of neurones in areas 17, 18 and 19. 7th International Neurobiology Meeting, Göttingen, Sept. 17th.

Gouras, P. and J. Kruger (1975). Colour selectivity of neurons in area 18 of monkey visual cortex. German Physiological Society, Vienna.

Green, D.G. (1968). The contrast sensitivity of the colour mechanisms of the human eye. Journal of Physiology, 196, 415-429.

Haber, R.N. and M. Herschenson (1973). The psychology of visual perception. Holt, Reinhardt and Winston.

Hajos, A. and N. Ritter (1965). Experiments to the problem of interocular transfer. Acta Psychologica, 24, 81-90.

Hajos, A. (1967). Psychophysiologische Probleme bei "Farbkonturen" und "Konturfarben". Symposium Über die Probleme der Wahrnehung, Bratislava, pp95-114.

Hajos, A. (1968). Psychophysiologische Probleme bei "Farbkonturen" und "Konturfarben". Studia Psychologica 10, 254-266.

Harris, C.S. (1969). Retinal location of orientation-specific colour after-effects. Journal of the Optical Society of America, 59, 504.

Harris, C.S. and A.R. Gibson (1968). Vision due to edge detectors, afterimages or "dipoles". Science, 162, 1506-1507.

Hebb, D.O. (1949). Organisation of Behaviour. John Wiley & Sons, Inc.

Heggelund, P. and A.-M. Hohmann (1976). Long-term retention of the "Gilinski-effect". Vision Research, 16, 1015-1017.

Held, R. and S.R. Shattuck (1971). Colour- and edge-sensitive channels in the human visual system: tuning for orientation. Science, 174, 314-316.

Henry, G.H., P.O. Bishop and B. Dreher (1974). Orientation, axis and direction as stimulus parameters for striate cells. Vision Research, 14, 767-777.

Hepler, N. (1968). Colour: a motion-contingent aftereffect. Science, 162, 376-377.

Hirsch, J. and G. Murch (1972). Variation in hue of a contour-contingent aftereffect due to colour adaptation during inspection of the stimulus patterns. Perception and Psychophysics, 11, 406-408.

Holding, D.H. and P.D. Jones (1976). Delayed one-trial extinction of the McCollough Effect. Quarterly Journal of Experimental Psychology, 28, 683-687.

Horn, G. (1967). Neuronal mechanisms of habituation. Nature, 215, 707-711.

Hubel, D.H. and T.N. Wiesel (1959). Receptive fields of single neurones in the cat's straite cortex. Journal of Physiology, 148, 574-591.

Hubel, D.H. and T.N. Wiesel (1962). Receptive fields, binocular interaction and functional architecture in the cat's visual cortex. Journal of Physiology, 160, 106-154.

Hubel, D.H. and T.N. Wiesel (1965). Receptive fields and functional architecture in two non-striate visual areas (18 and 19) of the cat. Journal of Neurophysiology, 28, 229-289.

Hubel, D.H. and T.N. Wiesel (1968). Receptive fields and functional architecture of monkey striate cortex. Journal of Physiology, 195, 215-243.

Hubel, D.H. and T.N. Wiesel (1977). Functional architecture of Macaque Monkey visual cortex. Proceedings of the Royal Society, B198, 1-59.

Kaneman, D. (1968). Method, findings and theory in studies of visual masking. Psychological Review, 70, 404-425.

Kruger, J. and P. Gouras (1975). Responses of cells in monkey striate cortex to patterns formed by differences in colour but not brightness. Proceedings of the German Physiological Society. Pflugers Archive Supplement to Vol. 355, p.191.

Leppman, P.K. (1973). Spatial frequency dependent chromatic after-effects. Nature 242, 411-412.

Lovegrove, W. (1976). Inhibition in simultaneous and successive contour interaction in human vision. Vision Research, 16, 1519-1521.

Lovegrove, W.J. and R. Over (1972). Colour adaptation of spatial frequency detectors in the human visual system. Science, 176, 541-543.

Lovegrove, W.J. and R. Over (1973). Colour selectivity in orientation masking and after-effect. Vision Research, 13, 895-902.

MacKay, D.M. (1970). Perception and Brain Function. (In: The Neurosciences: Second Study Programme. F.O. Schmitt, Editor-in-Chief), The Rockefeller University Press, New York.

MacKay, D.M. and V. MacKay (1973 (a)). Orientation-sensitive after-effects of dichoptically presented colour and form. Nature, 242, 477-479.

MacKay, D.M. and V. MacKay (1973 (b)). The time course of the McCollough Effect and its physiological implications. Journal of Physiology, 237, 38-39P.

MacKay, D.M. and V. MacKay (1974 (a)). Effects of sleep and darkness on the time-course of the McCollough Effect. (Abstract). Proc. Physiol. Soc., 69P, September.

MacKay, D.M. and V.MacKay (1974 (b)). Psychophysical evidence of neuronal plasticity in the primary visual pathway. (In: I.V.P.S. Symposium on Brain and Behaviour. New Delhi, Oct.).

MacKay, D.M. and V. MacKay (1975). What causes decay of pattern-contingent chromatic aftereffects. Vision Research, 15, 462-464.

MacKay, D.M. and V. MacKay (1977 (a)). Retention of the McCollough Effect in darkness: storage or enhanced read-out? Vision Research, 17, 313-317.

MacKay, V. and D.M. MacKay (1977 (b)). Multiple orientation-contingent chromatic aftereffects. Quarterly Journal of Experimental Psychology, 29, 203-219.

Mackworth, J.F. (1963). The duration of the visual image. Canadian Journal of Psychology, 17, 63-81.

May, J.G. (1972). Chromatic adaptation of orientation- and size-specific visual processes in man. Vision Research, 12, 1509-1517.

May, J.G., D.A. Leftwich and P. Aptaker (1974). Evoked potential correlates of adaptation to wavelength and orientation. Vision Research, 14, 143-146.

Mayhew, J.E.W. and S.M. Anstis (1972). Movement aftereffects contingent on colour, intensity and pattern. Perception and Psychophysics, 12, 77-85.

McCarter, A. and A.I. Silver (1977). The McCollough Effect: a classical conditioning phenomenon? Vision Research, 17, 317-321.

McCollough, C. (1965). Colour adaptation of edge-detectors in the human visual system. Science, 149, 1115-1116.

Mikaelian, H.H. (1975). Colour selectivity and interocular transfer of colour specific tilt aftereffects. Vision Research, 15, 157.

Mitchell, D.E., J. Reardon and D.W. Muir (1975). Interocular transfer of the motion after-effect in normal and stereoblind observers. Experimental Brain Research, 22, 163-173.

Mitchell, D.E. and C. Ware (1974). Interocular transfer of a visual after-effect in normal and stereoblind humans. Journal of Physiology, 236, 707-721.

Murch, G.M. (1972). Binocular relationships in a size and colour orientation-specific aftereffect. Journal of Experimental Psychology, 93, 30-34.

Murch, G.M. (1974). Colour contingent motion aftereffects: single or multiple levels of processing. Vision Research, 14, 1181-1184.

Murch, G.M. (1976). Classical conditioning of the McCollough Effect: temporal parameters. Vision Research, 16, 615-619.

Murch, G. (1977). A reply to McCarter and Silver. Vision Research, 17, p321-323.

Murch, G.M. and J. Hirsch (1972). The McCollough Effect created by complementary afterimages. American Journal of Psychology, 85, 241-248.

Neisser, V. (1968). Cognitive Psychology. Appleton Century Crofts.

Over, R., N. Long and W. Lovegrove (1973). Absence of binocular interaction between spatial and colour attributes of visual stimuli. Perception and Psychophysics, 13, 534-540.

Piggins, P.J. and P.K. Lepmann (1973). Role of retinal image motion in evoking the McCollough Effect. Nature, New Biology, 245, 255-256.

Poggio, G.F., R. Mansfield and A. Sillito (1971). Functional properties of neurons in the striate cortex of the macaque monkey subserving the foveal region of the retina. Society for Neurosciences. 1st Annual Meeting.

Regan, D. and C.W. Tyler (1971). Some dynamic features of colour vision. Vision Research, 11, 1307-1324.

Regan, D. and C.W. Tyler (1971). Temporal summation and its limits for wavelength changes: an analogue of Bloch's Law for colour vision. Journal of the Optical Society of America, 61, 1414-1421.

Riggs, L.A., K.D. White and P.D. Eimas (1973). The encoding and decay of orientation-contingent aftereffects of colour. Journal of the Optical Society of America, 63, 1287.

Riggs, L.A., K.D. White and P.D. Eimas (1974). Establishment and decay of orientation-contingent aftereffects of colour. Perception and Psychophysics, 16, 535-542.

Sanderson, K.J., P.O. Bishop and I. Darian-Smith (1971). The properties of the binocular receptive fields of L.G.N. neurones. Experimental Brain Research, 13, 178.

Sekuler, R. (1974). Spatial Vision. (In: Annual Review of Psychology, Ed. M. Rosengweig and L. Porter. Palo Alto: Annual Review, p.195-232).

Sharpe, C.R. (1974). The colour specificity of spatial adaptation: red-blue interactions. Vision Research, 14, 41-51.

Sharpe, C.R. and S. Mandl (1977). Colour inputs to orientation detectors in the human visual system. Vision Research, 17, 77-83.

Shattuck, S. and R. Held (1975). Colour and edge sensitive channels converge on stereo-depth analysers. Vision Research, 15, 309-311.

Shute, C.C.D. (1977 (a)). A device for measuring the McCollough Effect (ME) using polarised light. Journal of Physiology, 265, 2-3P.

Shute, C.C.D. (1977 (b)). Strength and decay of McCollough Effects. Journal of Physiology, 268, 34-35P.

Shute, C.C.D. (1978). Influence of centrally active drugs on the McCollough Effect. Proceedings of the Physiological Society. 11th February 1978, 54P.

Skowbo, D., T. Gentry and R.B. Morant (1974). The McCollough Effect: influence of several kinds of visual stimulation on decay rate. Perception and Psychophysics, 16, 47-49.

Skowbo, D., P.N. Timney, T.A. Gentry and R.B. Morant (1975). McCollough Effects: experimental findings and theoretical accounts. Psychological Bulletin, 82, 497-510.

Sperling, G. (1960). The information available in brief visual presentation. Psychological Monographs, 74, 1-29.

Spigel, I.M. (1960). The effects of differential post-exposure illumination on the decay of a movement after-effect. Journal of Psychology, 50, 209-210.

Stone, J. and R.B. Freeman (1973). Neurophysiological mechanisms in the visual discrimination of form. (In: Handbook of Sensory Physiology: Vol. VII/3 Pt. A. Ed. R. Jung, Springer-Verlag.

Stromeyer, C.F. (1969). Further studies of the McCollough Effect. Perception and Psychophysics, 6, 105-110.

Stromeyer, C.F. (1972). Contour-contingent colour aftereffects: retinal area specificity. American Journal of Psychology, 85, 227-235.

Stromeyer, C.F. (1972). Edge-contingent colour after-effects: spatial frequency specificity. Vision Research, 12, 717-733.

Stromeyer, C.F., S. Klein and C.E. Sternheim (1977). Is spatial adaptation caused by prolonged inhibition? Vision Research, 17, 603-606.

Timney, B.N., T.A. Gentry, D. Skowbo and R.B. Morant (1976). Threshold elevation following adaptation to colour gratings. Vision Research, 16, 601-607.

Timney, B.N., T.A. Gentry, D. Skowbo and R.B. Morant (1974). Chromatic grating thresholds and the McCollough Effect. Vision Research, 14, 1033-1035.

Uhlarik, J.J. and A.G. Osgood (1974). The role of some spatial parameters of gratings on the McCollough Effect. Perception and Psychophysics, 15, 524-528.

Vautin, R.G. and M.A. Berkley (1977). Responses of single cells in cat visual cortex to prolonged stimulus movement: neural correlates of visual aftereffects. Journal of Neurophysiology, 40, 1051-1066.

Virsu, V. and S. Haapasalo (1973). Relationships between channels for colour and spatial frequency in human vision. Perception, 2, 31-40.

White, K.D. and S.R. Ellis (1975). McCollough Effect: pattern alternation rate influences establishment. Journal of the Optical Society of America, 65, 1200.

White, K.D. (1976). Studies of orientation-contingent color aftereffects. Ph.D. Thesis, Brown University.

Wyatt, H.J. (1974). Single and doubly contingent after-effects involving colour, orientation and spatial frequency. Vision Research, 14, 1185-1193.

Zeki, S.M. (1973). Colour coding in rhesus monkey prestriate cortex. Brain Research, 53, 422-427.

Zeki, S.M. (1974). Functional organization of a visual area in the posterior bank of the superior temporal sulcus of the rhesus monkey. Journal of Physiology, 236, 549.