Article:

Thompson, Peter Gage and Movshon, Anthony (1978) Storage of spatially specific threshold elevation. Perception. pp. 65-73. ISSN 0301-0066

Perception, 1978, volume 7, pages 65-73

Storage of spatially specific threshold elevation

Peter G Thompson¶, J Anthony Movshon§
The Psychological Laboratory, Downing Street, Cambridge CB2 3EB, England
Received 7 March 1977

Abstract. The decay of several visual aftereffects may be prolonged by interposing a period of light-free or pattern-free viewing between adaptation and testing. We demonstrate that this storage phenomenon can be observed using the threshold elevation aftereffect that follows inspection of a high-contrast grating pattern. Control experiments comparing thresholds for vertical and horizontal gratings after adaptation to a vertical grating reveal that the stored aftereffect, like its unstored counterpart, is pattern-selective. Storage is equally pronounced with stimuli that are detected by pattern-analyzing or movement-analyzing visual channels. Unlike other aftereffects, the threshold-elevation aftereffect requires that the storage period be light-free; no storage is seen if a blank field is inspected between adaptation and testing. The results are discussed with respect to the nature of visual aftereffects, and possible cognitive or physiological models of storage.

1 Introduction

The visual perception of pattern, movement, and color may be strongly affected by prior exposure to certain kinds of visual stimuli. The best known of these visual aftereffects is the aftereffect of seen movement: after inspection of a moving pattern, similar patterns, when stationary, appear to move in a direction opposite to the adapting motion (Purkinje 1825; Exner 1888; Wohlgemuth 1911). This, and a number of other aftereffects [e.g. the pattern-selective color aftereffect discovered by McCollough (1965)] show the phenomenon of *storage.* If the aftereffect is induced by adapting for 1 min to a moving pattern, an immediately viewed test pattern appears to move for a few tens of seconds. If, however, a period of darkness is interposed between the adaptation and test periods, an apparently normal aftereffect may be seen, even after many minutes or hours of darkness (Wohlgemuth 1911; Spigel 1960; Honig 1967; Masland 1969; Thompson, in preparation). Even more prolonged storage of the McCollough aftereffect has been reported by Skowbo et al (1974), MacKay and MacKay (1975) and Jones and Holding (1976).

No satisfactory theory has been put forward to account for this phenomenon, and we felt that this is in part due to the fact that neither the movement or McCollough aftereffect has a well understood physiological basis (but see Barlow and Hill, 1963). There is another visual aftereffect, first reported by Gilinsky (1968), Pantle and Sekuler (1968) and Blakemore and Campbell (1969a), for which a sound physiological theory exists, and we decided to examine this aftereffect for storage.

The aftereffect is a simple one: following inspection of a high-contrast grating pattern, the minimum contrast necessary for detection of the same or similar gratings is raised by a factor of about five. This aftereffect is widely thought to result from the desensitization of pattern-specific neurons in the visual cortex. The specificities of the aftereffect for spatial frequency and orientation correspond closely to the orientation and spatial selectivities of striate cortical neurons (Blakemore and Campbell 1969b; Blakemore and Nachmias 1971; Hubel and Wiesel 1962, 1968;

¶Present address: Department of Psychology, University of York, York, England
§Present address and address for reprint requests: Department of Psychology, New York University, 6 Washington Place, Room 1173, New York, New York 10003 USA

Campbell et al 1968; Campbell et al 1969); moreover, Maffei et al (1973) have shown that the sensitivity of individual cortical neurons is affected by adaptation in a manner similar to the way in which human observers' sensitivity is affected by that adaptation.

The experiments described below reveal that this aftereffect shows the phenomenon of storage, and examine some of the conditions necessary for that storage. We have presented these results to the Experimental Psychology Society (Thompson and Movshon 1975).

2 Methods

Our methods for displaying steady or temporally modulated grating patterns on the face of display oscilloscopes were similar to those described by Schade (1956), Campbell and Green (1965), and Robson (1966). All the gratings had a sinusoidal luminance profile in a direction orthogonal to their component stripes. The *spatial frequency* of a grating is the number of cycles subtending 1 deg of visual angle, and its *contrast* is the difference between the maximum and minimum luminances in the grating divided by their sum. Our adapting patterns were always vertical and had a contrast of 0·7. Test patterns could be either vertical or horizontal, and their contrast was controlled by the subject through a high-precision logarithmic potentiometer, which was ganged to a linear potentiometer connected to a digital voltmeter and printer, providing a direct measure of grating contrast in logarithmic units.

In experiment 1, we used the screen of a single Solartron CD1400 oscilloscope for the presentation of test and adapting gratings; its space-average luminance was always 4·2 cd m^{-2}. In later experiments, two Telequipment D83 oscilloscopes were used; their screen luminance was 53 cd m^{-2}. The screens were masked by circular apertures 4·5 deg in diameter, separated vertically (when two screens were used) by 2 deg. The dim background luminance was 0·07 cd m^{-2} throughout. During adaptation to stationary gratings, subjects were instructed to move their eyes around a thin 0·5 deg fixation circle at the center of the screen to prevent the formation of conventional afterimages.

Rather than adopting the 'tracking' procedure used by Blakemore and Campbell (1969b) in their investigation of the decay of the aftereffect, our subjects made discrete threshold settings once every 10 s, reducing the grating's contrast below threshold between settings. Each setting took 4 s or less. We ran each experimental condition four times for each subject; each data point thus represents the logarithmic mean of settings made on four independent trials; the standard error of this mean rarely exceeded 0·1 log unit.

On the basis of pilot studies, and the decay data provided by Blakemore and Campbell (1969b) and Blakemore et al (1973), we used an initial adaptation period of 1 min in all cases. This period is sufficient for the magnitude of the aftereffect to reach its maximum level, and gives a decay time under normal circumstances of between 30 s and 60 s. In nonstorage control trials, the test period began immediately after the offset of the adapting grating; in storage trials, the test period began after a variable period of storage. The four experiments differed in the stimulus parameters used, the nature of the control data, and the nature of the storage interval.

2.1 *Subjects*

Most of the data were obtained from the two authors, but the substance of the findings was verified with four other experienced observers. All subjects viewed the screens binocularly through their normal refraction, without artificial pupils.

3 Results

3.1 *Experiment 1. Does threshold elevation show storage?*

In this and the two following experiments, the storage period was one of darkness: after the offset of the adapting pattern, the subject closed his eyes for a variable period and then began the test period. The control condition in this experiment was one in which the adaptation pattern was a blank field of the same mean luminance as the test patterns. All the gratings in this experiment had a spatial frequency of 5 cycles deg^{-1}, and were steadily presented.

The results obtained from both subjects in this experiment were similar, and those from JAM are illustrated in figure 1. The uppermost graph shows the decay of the aftereffect in a nonstorage condition. The solid symbols connected by solid lines show that threshold declined over a 30 s period at the end of the adaptation to near-baseline levels; the open symbols show data for the control condition, in which a blank field was substituted for the adapting grating. The solid symbols linked by broken lines show the storage of the aftereffect, and are taken from the data shown in the four lower graphs. These show data for four durations of storage, indicated by the solid blocks. The dashed lines on each graph reproduce the baseline data from the upper graph; the open symbols continue to represent data obtained from trials in which the observer adapted to a blank screen rather than a grating. The initial data point from each of these graphs is shown, linked to the others by dashed lines, on the upper graph.

It may readily be seen that the aftereffect showed storage. After a 30 s or 60 s storage period (in which time the threshold would have returned to baseline in a nonstorage condition) the initial threshold settings were two to three times higher than the control settings. Even after longer storage periods (120 or 240 s), the initial thresholds were still above baseline levels. It is also apparent from the control data that merely sitting in darkness for this length of time also elevates threshold to some degree; this effect is presumably related to the light adaptation necessary after

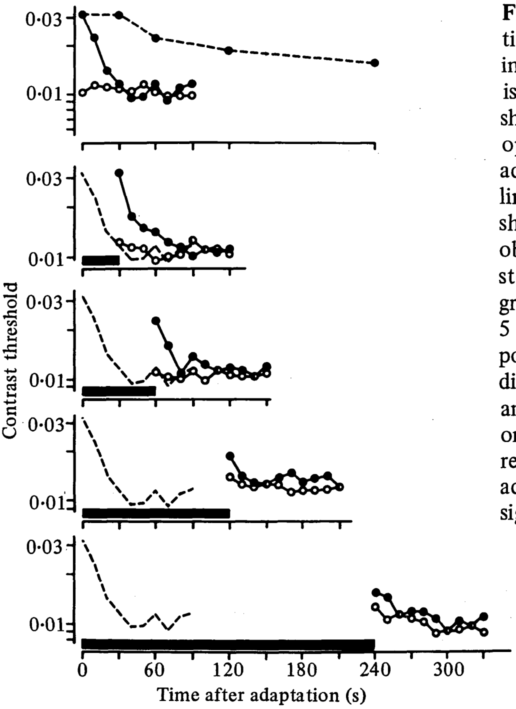

Figure 1. Contrast thresholds obtained at various times after adaptation, with and without an interposed period of darkness (whose duration is indicated by the solid blocks). Solid symbols show data obtained after grating adaptation, open symbols show data obtained after adaptation to a blank field. The solid symbols linked by broken lines in the uppermost graph show the means of the threshold settings obtained immediately after the different storage periods represented in the lower four graphs. Subject JAM, spatial frequency 5 cycles deg^{-1}, steady presentation. Each point is the mean of four settings. The small differences between the grating-adaptation and blank-adaptation conditions after more than one minute of testing probably reflect a small residual adaptation effect from previous adaptation sessions, and are of doubtful significance.

opening the eyes, and was accompanied by subjective impression of glare on the first few trials. Nevertheless, even after long storage periods thresholds were more elevated after grating adaptation than they were after blank adaptation. These data are summarized by the solid symbols linked by broken lines in the upper graph, which reveal that the decay of the aftereffect may be prolonged by a factor of five or so by the interposed period of darkness.

3.2 *Experiment 2. Is storage pattern-specific?*

We did not feel that the data from experiment 1 represented a convincing demonstration of *pattern-specific* storage, since the possibility existed that we were observing a nonspecific effect of the storage period and not a true extension of the duration of the aftereffect. In order to check this possibility, we adopted a new control condition, in which the adaptation field always contained a high-contrast vertical grating, but in which the test field was alternately a vertical or a horizontal grating, trial by trial. Since the aftereffect is sufficiently orientation-selective that threshold elevation at an orientation orthogonal to the adapting orientation is negligible (Blakemore and Campbell 1969a; Movshon and Blakemore 1973), this procedure controlled for any nonspecific effects contaminating the results of experiment 1.

The data for the two subjects were again similar, and those for JAM are shown in figure 2. The format of this figure is very similar to that of figure 1, save that the open symbols here represent the thresholds for a horizontal grating presented after adaptation to a vertical grating. The storage revealed in figure 1 is clearly preserved under the new control condition; in every case, the thresholds for vertical gratings were more elevated than those for horizontal gratings, even when the duration of the storage period greatly exceeded the decay period of the unstored aftereffect.

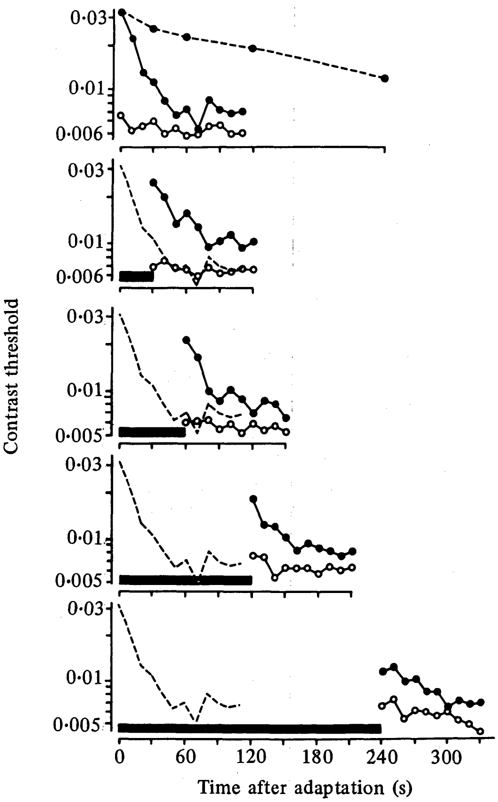

Figure 2. Similar to figure 1, except that open symbols here represent data obtained with a horizontal test grating while solid symbols represent data obtained with a vertical test grating; the adapting grating was always vertical, and here, as in figure 1, the small residual differences between thresholds in the two test conditions after long test periods may be attributed to small long-lasting adaptation effects of uncertain significance. Subject JAM, spatial frequency 5 cycles deg^{-1}, steady presentation.

We had difficulty in convincing some of our colleagues of the validity of these results, so in order to convince them and add generality to our findings, we examined storage in four observers other than ourselves, using a 60 s storage period. The results for these subjects are shown in figure 3. The left-hand graph of each pair represents the nonstorage control condition; the right-hand graph shows results for the storage condition. Despite the rather more variable performance of these unpracticed subjects, clear storage was present in each case. We should stress that these data were obtained in the first and only session for each subject, and that no subject's data have been omitted.

3.3 *Experiment 3. Do pattern and movement channels store differently?*

We felt at this point that we had demonstrated the existence of storage of this aftereffect to our satisfaction. We were interested, however, in the rather short duration of the storage. While the effects shown in figures 1 and 2 declined to a fraction after only 4 min of storage, previous reports of storage in the movement aftereffect claimed effects of much longer duration (Spigel 1960; Honig 1967; Masland 1969; Thompson, in preparation). It seemed to us that the reason for this difference might lie in the different behavior of movement-detecting and pattern-detecting mechanisms in the visual system. Kulikowski and Tolhurst (1973) and Tolhurst (1973) provided evidence for the existence of two classes of detection channel in human vision: 'pattern' channels, most sensitive to high spatial frequencies

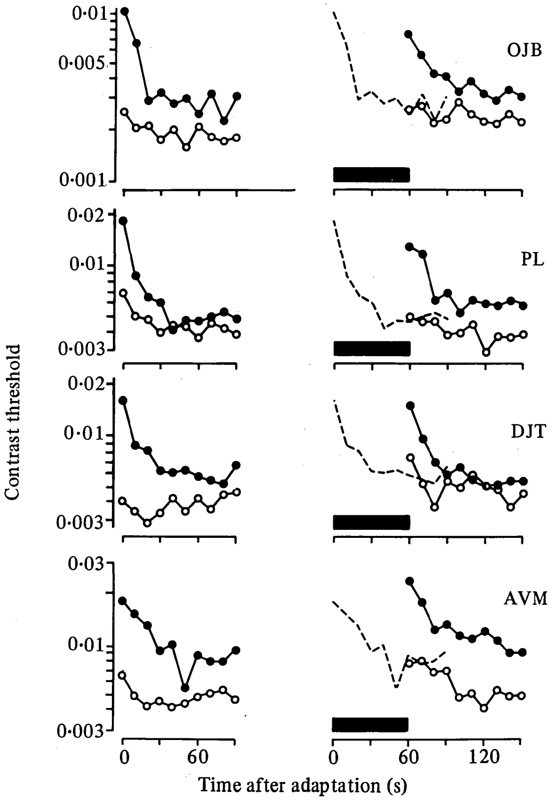

Figure 3. Contrast thresholds obtained at various times after adaptation from four observers. The left-hand graph of each pair shows decay of the unstored aftereffect; the right-hand graph shows the stored aftereffect. Conventions, symbols, and stimulus conditions as in figure 2.

and stationary patterns, and 'movement' or 'flicker' channels, most sensitive to low spatial frequencies and insensitive to steady patterns. From their data, it seemed likely that the 5 cycles deg^{-1} steady grating used in experiments 2 and 3 would have been detected solely by the 'pattern' channels, while the movement aftereffect and its prolonged storage might more reasonably be attributed to the 'movement' channels. By repeating Kulikowski and Tolhurst's (1973) experiment on 'flicker' and 'pattern' thresholds, we found that under our conditions a grating of 1 cycle deg^{-1} sinusoidally modulated at 5 Hz was detected with 'flicker' channels by both our subjects (its appearance at threshold was indefinite, and about 0·5 log unit of suprathreshold contrast was necessary for its spatial structure to become visible). We therefore repeated experiment 2 using these stimulus parameters, in the hope that this would reveal any difference in storage between pattern-detecting and movement-detecting visual mechanisms.

Our findings are shown in figure 4, this time for PGT. The control condition was that used in experiment 2 (vertical and horizontal test gratings). The data reveal that storage under these conditions is not so prolonged as that of the movement aftereffect, and closely resembles the storage seen with 'pattern'-channel detected stimuli. After a storage period of 240 s, the difference in threshold elevation between vertical and horizontal test gratings had declined to a fraction of its initial value.

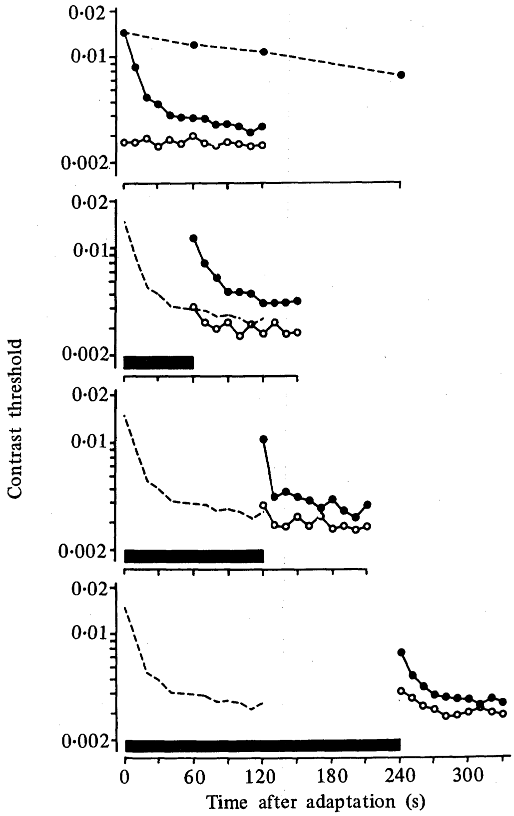

Figure 4. Similar to figure 2. Subject PGT, spatial frequency 1 cycle deg^{-1}, sinusoidal contrast modulation at 5 Hz.

3.4 *Experiment 4. Is darkness necessary for storage?*

In our final experiments, we examined the nature of the visual exposure necessary to obtain storage. It has been reported that the movement aftereffect stores well either when the storage period is one of darkness, or when it is a period in which the observer inspects an unpatterned illuminated field (Spigel 1962; Honig 1967). This suggests that it is necessary to *observe* the aftereffect in order to abolish it; only inspection of a pattern against which the aftereffect may be manifested is sufficient. We felt that this might not be the case with the threshold elevation aftereffect, for two reasons. First, the aftereffect may not really be said to be 'expressed' in the same manner as the movement aftereffect, since near-threshold stimuli have an identical appearance before and after adaptation; second, if perceived contrast were somehow acting to abolish the aftereffect, it seemed unlikely to us that the minimal contrast visible during a nonstorage control trial (during which the subject saw a near-threshold grating for a few seconds in every ten) would suffice. Rather, the mere presence of the illuminated field might be responsible for the decay of the aftereffect.

We examined storage, then, in a condition in which the subject did not close his eyes during the storage period, but transferred his gaze to a large (40 deg x 40 deg) blank field illuminated so that its luminance and color closely matched those of the oscilloscope faces. We used both 'pattern' (experiments 1 and 2) and 'flicker' (experiment 3) stimuli in these experiments. The results were uniformly negative: for no stimulus condition or storage duration could we demonstrate any convincing storage. We conclude that the period intervening between adaptation and test periods must be one of darkness in order to demonstrate storage of threshold elevation. We have not systematically examined how much illumination is necessary to prevent storage, but we feel that very little light would suffice.

4 Discussion

Our results show that the threshold elevation aftereffect, an aftereffect whose physiological substrate is thought to be well understood, shows the mystifying phenomenon of storage. Similar evidence, obtained under less well-controlled conditions, has been presented by Heggelund and Hohmann (1976).

The storage of this aftereffect differs in two ways from the previously reported storage of the movement aftereffect. First, the duration of storage is less prolonged, although longer adaptation periods might yield more pronounced storage (Heggelund and Hohmann 1976; Iverson and Pavel, in preparation). Second, while the movement aftereffect stores well against a light unpatterned field, storage of threshold elevation is abolished by light. We feel that the explanation for these discrepancies might lie in the nature of the aftereffects themselves. Threshold elevation as we have measured it is not accompanied by any change in the perception of the visual world: low-contrast patterns become less visible, but *threshold* patterns have a similar appearance before and after adaptation. The movement aftereffect, on the other hand, is an effect that may only be measured perceptually (though it has other correlates: Tolhurst et al, 1973; Thompson 1976, in preparation). It may be, then, that the difference lies in the difference between threshold and suprathreshold aftereffects. Threshold elevation has three suprathreshold correlates: the tilt aftereffect (Gibson and Radner 1937; Campbell and Maffei 1971), the perceived spatial frequency shift (Blakemore et al 1970), and the reduction in perceived contrast of suprathreshold stimuli after adaptation (Blakemore et al 1973). We have preliminary data suggesting that the storage of the tilt aftereffect more nearly resembles that of threshold elevation than that of the movement aftereffect, but it would be worthwhile to examine any or all of these effects for storage in order to test the notion that they share a common substrate.

4.1 *The nature of storage*

It seems to us that two kinds of explanation for the storage phenomenon might be sought. One kind of account has its basis in the phenomena of conditioning and learning, and draws parallels between the extensive literature in this area and the phenomenon of storage (Mayhew and Anstis 1972; Skowbo et al 1974; Heggelund and Hohmann 1976). In this kind of model, storage is linked in some way with the observer's memory of recently seen stimuli; this memory influences his perception of subsequently viewed stimuli. We find this class of model uncongenial because we have demonstrated storage of an aftereffect in the absence of any perceptual cue that might lead to the required 'association'. Indeed, while it is conceivable that prior conditioning could alter an observer's *perception* of a given stimulus, it is less clear that it should by simple association cause a change in *detection* threshold, since near-threshold stimuli look the same before and after adaptation.

We prefer to seek an explanation for storage within the conventional confines of the visual system, in the nature of the adaptation process itself. While it is possible that simple models representing adaptation as a fatigue process are inadequate (Dealy and Tolhurst 1974), we see no reason to doubt that the expression of the stored aftereffect, like its unstored counterpart, may be seen at the level of single visual cortical neurons (Maffei et al 1973). It seems reasonable that, as suggested by Dealy and Tolhurst, the threshold-elevation aftereffect is related to the prolonged activity of inhibitory mechanisms in the visual cortex. Storage does not force us to seek explanations for visual aftereffects in the realm of cognition, but may present us with information about the nature of intracortical inhibitory processes in primary visual centers. This notion is open to experimental test, and we are currently undertaking appropriate neurophysiological studies of single striate cortical neurons.

Acknowledgements. This work was supported in part by a Programme Grant from the Medical research Council to Colin Blakemore (number G973/463B). JAM held a Research Training Scholarship from the Wellcome Trust, and PGT was a Social Sciences Research Council Scholar. Preparation of the manuscript was partly supported by a grant to JAM from the National Science Foundation (number BNS76-18904). We are grateful to John Robson, David Tolhurst, and Oliver Braddick for helpful discussion, and to our subjects for their time and skepticism.

References

Barlow H B, Hill R M, 1963 "Evidence for a physiological explanation of the waterfall phenomenon and figural aftereffects" *Nature (London)* **200** 1345-1347

Blakemore C, Campbell F W, 1969a "Adaptation to spatial stimuli" *Journal of Physiology (London)* **200** 11P-13P

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

Blakemore C, Muncey J P J, Ridley R M, 1973 "Stimulus specificity in the human visual system" *Vision Research* **13** 1915-1931

Blakemore C, Nachmias J, 1971 "The orientation specificity of two visual aftereffects" *Journal of Physiology (London)* **213** 157-174

Blakemore C, Nachmias J, Sutton P, 1970 "The perceived spatial frequency shift: evidence for frequency-selective neurones in the human brain" *Journal of Physiology (London)* **210** 727-750

Campbell F W, Cleland B G, Cooper G F, Enroth-Cugell C, 1968 "The angular selectivity of visual cortical cells to moving gratings" *Journal of Physiology (London)* **198** 237-250

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

Campbell F W, Green D G, 1965 "Optical and retinal factors affecting visual resolution" *Journal of Physiology (London)* **181** 576-593

Campbell F W, Maffei L, 1971 "The tilt aftereffect: a fresh look" *Vision Research* **11** 833-840

Dealy R S, Tolhurst D J, 1974 "Is spatial adaptation an aftereffect of prolonged inhibition?" *Journal of Physiology (London)* **241** 261-270

Exner S, 1888 "Einige Beobachtungen über Bewegungsnachbilder" *Zentralblatt für Physiologie* **1** 135-140

Gibson J J, Radner M, 1937 "Adaptation, after-effect and contrast in the perception of tilted lines. I. Quantitative studies" *Journal of Experimental Psychology* **20** 453-467

Gilinsky A S, 1968 "Orientation specific effects of patterns of adapting light on visual acuity" *Journal of the Optical Society of America* **58** 13-18

Heggelund P, Hohmann A, 1976 "Long-term retention of the 'Gilinsky-effect'" *Vision Research* **16** 1015-1017

Honig W K, 1967 "Studies of the storage of the after-effect of seen movement" paper presented to the Psychonomics Society, Chicago, Ill.

Hubel D H, Wiesel T N, 1962 "Receptive fields, binocular interaction and functional architecture in the cat's visual cortex" *Journal of Physiology (London)* **160** 106-154

Hubel D H, Wiesel T N, 1968 "Receptive fields and functional architecture of monkey striate cortex" *Journal of Physiology (London)* **195** 215-243

Jones P D, Holding D H, 1976 "Extremely long-term persistence of the McCollough effect" *Journal of Experimental Psychology, Human Perception and Performance* **1** 323-327

Kulikowski J J, Tolhurst D J, 1973 "Psychophysical evidence for sustained and transient detectors in human vision" *Journal of Physiology (London)* **232** 149-162

McCollough C, 1965 "Color adaptation of edge detectors in the human visual system" *Science* **149** 1115-1116

MacKay D M, MacKay V, 1975 "What causes decay of pattern-contingent chromatic aftereffects?" *Vision Research* **15** 462-464

Maffei L, Fiorentini A, Bisti S, 1973 "Neural correlate of perceptual adaptation to gratings" *Science* **182** 1036-1038

Masland R, 1969 "Visual motion perception: experimental modification" *Science* **165** 819-821

Mayhew J E W, Anstis S M, 1972 "Movement aftereffects contingent on color, intensity and pattern" *Perception and Psychophysics* **12** 77-85

Movshon J A, Blakemore C, 1973 "Orientation specificity and spatial selectivity in human vision" *Perception* **2** 53-60

Pantle A J, Sekuler R W, 1968 "Size-detecting mechanisms in human vision" *Science* **162** 1146-1148

Purkinje J, 1825 cited in Wohlgemuth (1911)

Robson J G, 1966 "Spatial and temporal contrast sensitivity of the visual system" *Journal of the Optical Society of America* **56** 1141-1142

Schade O H, 1956 "Optical and photoelectric analog of the eye" *Journal of the Optical Society of America* **46** 721-739

Skowbo D, Gentry T, Timney B, Morant R B, 1974 "The McCollough effect: influence of several kinds of visual stimulation on decay rate" *Perception and Psychophysics* **16** 47-49

Spigel I M, 1960 "The effects of differential post-exposure illumination on the decay of a movement aftereffect" *Journal of Psychology* **50** 209-210

Spigel I M, 1962 "Contour absence as a critical factor in the inhibition of the decay of a movement aftereffect" *Journal of Psychology* **54** 221-228

Thompson P G, 1976 "Velocity aftereffects and the perception of movement" PhD thesis, University of Cambridge, England

Thompson P G, Movshon J A, 1975 "Storage of the threshold elevation aftereffect" paper presented to the Experimental Psychology Society, Oxford, April

Tolhurst D J, 1973 "Separate channels for the analysis of the shape and movement of a moving visual stimulus" *Journal of Physiology (London)* **231** 385-402

Tolhurst D J, Sharpe C R, Hart G, 1973 "The analysis of the drift rate of moving sinusoidal gratings" *Vision Research* **13** 2545-2555

Wohlgemuth A, 1911 "On the aftereffect of seen movement" *British Journal of Psychology Monograph Supplement* **1** 1-117