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Adaptation and Aftereffects in the Visual System

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Statement

The research contained in this thesis was produced solely by the author, under the supervision of Pascal Mamassian and David Simmons. The thesis was composed by the stated author Lisa O'Kane. Sections of the findings have been presented in abstract form at the annual Vision Sciences Society conference in Sarasota, Florida (2004, 2005 & 2006) and Applied Visual Association Christmas Meeting, 2005.

Abstract

This thesis is concerned with the investigation of the nature of adaptation and aftereffects in the human visual system. We extend previous research first by specifically investigating the temporal aspect of these processes. The technique we develop and present here offers a method of measuring the temporal dynamics of visual aftereffects which captures how the aftereffect is varying in both strength and duration. In the first experimental chapter we present data following the application of this technique to the Depth After Effect. We then go on to apply this technique to the investigation of the Motion After Effect and in particular look at the temporal dynamics of this effect using different stimuli during adaptation. The results of this form the second and third experimental chapter of this thesis. Having addressed aspects of the nature of visual aftereffects to both motion and disparity, we then present an experiment looking at adaptation to both motion *and* disparity, and the effect this has on an ambiguous stimuli, that of a transparent surface. We found that observers' biases for which direction of motion moved in front was influenced in a manner mostly consistent with a depth-contingent motion aftereffect following adaptation. These results emphasize the critical role of neural structures sensitive to both motion and binocular disparity in the perception of motion transparency. In summary, this thesis addresses the nature of visual aftereffects and also presents a method of measuring how they vary with time.

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Chapter 1: Overview and Introduction

1.1 Overview

Visual after-effects are among the most striking and unexpected phenomena of our visual experience. It is also a concept best understood through experience. Take a moment to glance at Fig. 1., which is an example of the Tilt After-Effect and the Spatial Frequency After-Effect.

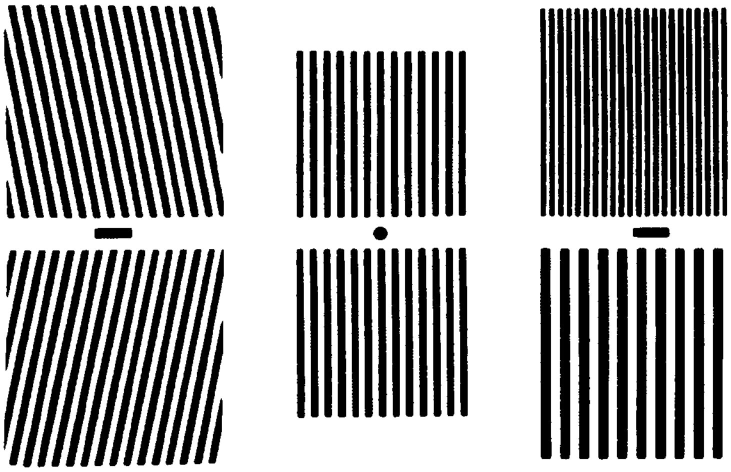

Fig 1. Adaptation by fixating on the bar between the left hand gratings will cause subsequent viewing of the middle image to appear tilted in the opposite direction of the grating first viewed. This is known as the Tilt After-Effect. Similarly, fixating on the bar in the middle of the right hand image for a period of time will cause the top image in the centre to appear at a lower spatial frequency and the bottom grating in the centre a higher spatial frequency. This is known as the Spatial Frequency After-Effect. Image taken from Barlow & Mollon (1982).

Although visual after-effect phenomena have fascinated philosophers and natural scientists for centuries, and generated vigorous interest among vision scientists for decades, a full theoretical understanding of their cause is still elusive (Anstis, Verstraten & Mather, 1998). These phenomena are thought to be responsible for these effects and research using after-effects and adaptation as experimental tools has contributed significantly to our understanding of the visual system. However, the processes underlying these effects remain a puzzle.

As theoretical advancement leads to an even more complex view of the nature of adaptation, possibly including multiple sites in the brain, detailed examination of after-effects provides an ideal opportunity to investigate the dynamic plasticity exhibited by the brain (Nishida & Ashida, 2000). A definition of dynamic plasticity is the rapid alteration in the response of the brain contingent on the changing input environment.

The topic of this thesis, therefore, is the temporal dynamics of visual after-effects. We also investigate the nature of contingent after-effects.

1.2 Introduction

After-effects have been described as the "psychophysicist's micro-electrode" (Frisby, 1979). The phenomena are thought to be the result of a process known as adaptation whereby a perceptual system responds to changes in its environment. Consequently, the study of after-effects, as well as being fascinating in its own right, also provides a window through which to view the plasticity of perceptual systems in response to ever-changing surroundings. Furthermore, because after-effects reflect the occurrence of underlying brain changes in response to the environment, they can also be used for revealing neural processes and connectivity.

Learning can be viewed as the act, process or experience of gaining knowledge or a skill (wordnet.Princeton.edy/perl/webwm). In trying to understand how this change takes place, adaptation could be important as it is a process by which the response of a system changes as a direct consequence of the input into the system. It may therefore be a process that is fundamental to learning and other conditioned behaviour. It is therefore of vital importance to develop a theoretical framework in which to understand this process.

Of course, the adaptation paradigm has been utilised to produce a wealth of data but it has been argued that advancement and understanding of the underlying theoretical issues have been impeded by inconsistent technique and poor methodology (Pantle, 1998). This research, therefore, is an attempt to overcome some of these drawbacks by using a novel technique for the examination of the temporal dynamics of visual after-effects and by investigating contingencies between after-effects.

This novel technique involves measuring the after-effect induced by adaptation at multiple time points using a variety of test stimuli. By correlating the measured response with the strength of the test stimulus, a full picture of the temporal dynamics of the after-effect can be built up. The application of this technique has delivered robust results in three areas. Firstly, when measuring the depth after-effect, a clear picture of the variation of the after-effect in time was produced. Utilising the technique it was possible to predict the strength of the after-effect in a given individual, given a certain degree of adaptation. This is a novel contribution to the field and allows for the objective quantification of this subjective phenomenon. The results revealed a clear relationship between the amount of disparity in the test stimulus and the perception of depth following adaptation. Specifically, the results were consistent with a linear relationship, showing depth perception directly dependent on disparity levels in the test stimulus.

Secondly, the technique was applied to the area of motion perception. We report that when measuring differences between after-effects in movement and depth, it became clear that the mechanisms underlying the movement after-effects were arguably more complex than those underlying the depth after-effect. For example, at least two systems appeared to underlie movement after-effects, elicited by different speeds and stimuli. Even more intriguing was the fact that the temporal variation of the movement after-effects deviated significantly from those obtained in depth processing despite using the same technique. The two key differences were that firstly, the data could not be fully characterised by a linear dependence of duration on test speed, and secondly, that there were less marked individual differences. For future purposes, an extension to this work would be to model the differences in temporal dynamics between movement and depth after-effects.

The third significant finding of this research thesis concerned adaptation in response to both motion and depth stimuli performed in an ambiguous context. This was a contingent after-effect experiment that has strong links to learning associations between stimuli and its effect on novel stimuli. The results indicated a relationship between motion and depth that influence perception of ambiguous new stimuli in a predictable manner. Consequently, this work has links to learning and the processes governing perception. Furthermore, these results indicate that learning can be influenced by simple exposure and can even influence experience of novel stimuli. This work, therefore, has implications for the nature of learning over time and in novel situations.

Having developed the technique and obtained results consistent with a measure of an after-effect decay we have substantiated a method by which full temporal variation of after-effects can be captured. The technique contributes to current research focusing on the underlying mechanisms of adaptation. The results presented in this research suggest the existence of non-identical mechanisms in the visual system, which underlie adaptation in general with respect to motion and depth. In order to capture these differences it is necessary to develop a framework for understanding adaptation and the main contribution of this work is a method that makes provision for this via the accurate measurement of the strength and temporal dynamics of visual after-effects.

Chapter 2: Literature Review

2.1 Historical importance of adaptation

When considering visual adaptation the key historical development was possibly the discovery that cells in the mammalian visual cortex respond selectively to properties of visual stimuli such as orientation, direction of motion and spatial frequency (Hubel & Wiesel, 1962). Following the logic that similar mechanisms exist in the human visual cortex, adaptation experiments have been used as a tool for investigating the selectivity and tuning of these visual filters, or channels (Anstis, 1998).

Consequently, adaptation experiments have contributed to the finding that selective mechanisms exist for orientation and spatial frequency in the human visual cortex. An early example of this is the significant finding by Blakemore & Campbell (1969) that demonstrated the change in the contrast sensitivity function (CSF) following adaptation to a sine-wave grating of a particular spatial frequency. It was found that contrast thresholds were only elevated for a limited range of spatial frequencies close to the adaptation frequency. This led to the conclusion that the adaptation process had isolated a 'channel' in the brain and that the CSF was the envelope of a number of overlapping spatial frequency selective channels. They also demonstrated that contrast adaptation is orientation specific, indicating that channels are tuned to both orientation and spatial frequency. Furthermore, following adaptation to a sine-wave grating of a particular spatial frequency, a subsequently viewed grating of a lower spatial frequency appeared to be lower still and conversely a grating of higher spatial frequency appeared to be of an even higher spatial frequency.

In a closely related set of experiments, Blakemore & Sutton (1969) demonstrated the presence of spatial frequency channels. They showed that adaptation of a particular channel shifts the peak sensitivity away from the test channel. They explained their results by saying that adaptation to a lower spatial frequency channel reduces the response in that channel to the test spatial frequency and so shifts the peak away from the adapting spatial frequency (see Fig 2 & Fig 3).

These experiments have helped make a fundamental contribution to our understanding of visual processing in that there are selective mechanisms in the human brain in respect of orientation and spatial frequency. These results have complemented those from physiological studies.

In applying the technique of adaptation, fundamental theories of vision have been challenged and an example of this would be to cite the demonstration of a negative colour after-effect that has made an important contribution to the understanding of colour vision (Goldstein, 2007). This is a parsimonious and critical demonstration that opponent-colour mechanisms contribute to colour perception and that colour vision cannot be explained solely in terms of the relative excitations of three wavelength-selective mechanisms (i.e. the original theory of trichromacy).

Another after-effect which has generated much research, is that observed following adaptation to motion. The movement after-effect (MAE) is one of the first unusual visual phenomena to be properly described, being first noticed, as far as we know, by Aristotle (see Anstis et al, 1998). Certainly, a description of visual motion adaptation occurred even before descriptions of apparent motion were made (Wohlgemuth, 1911).

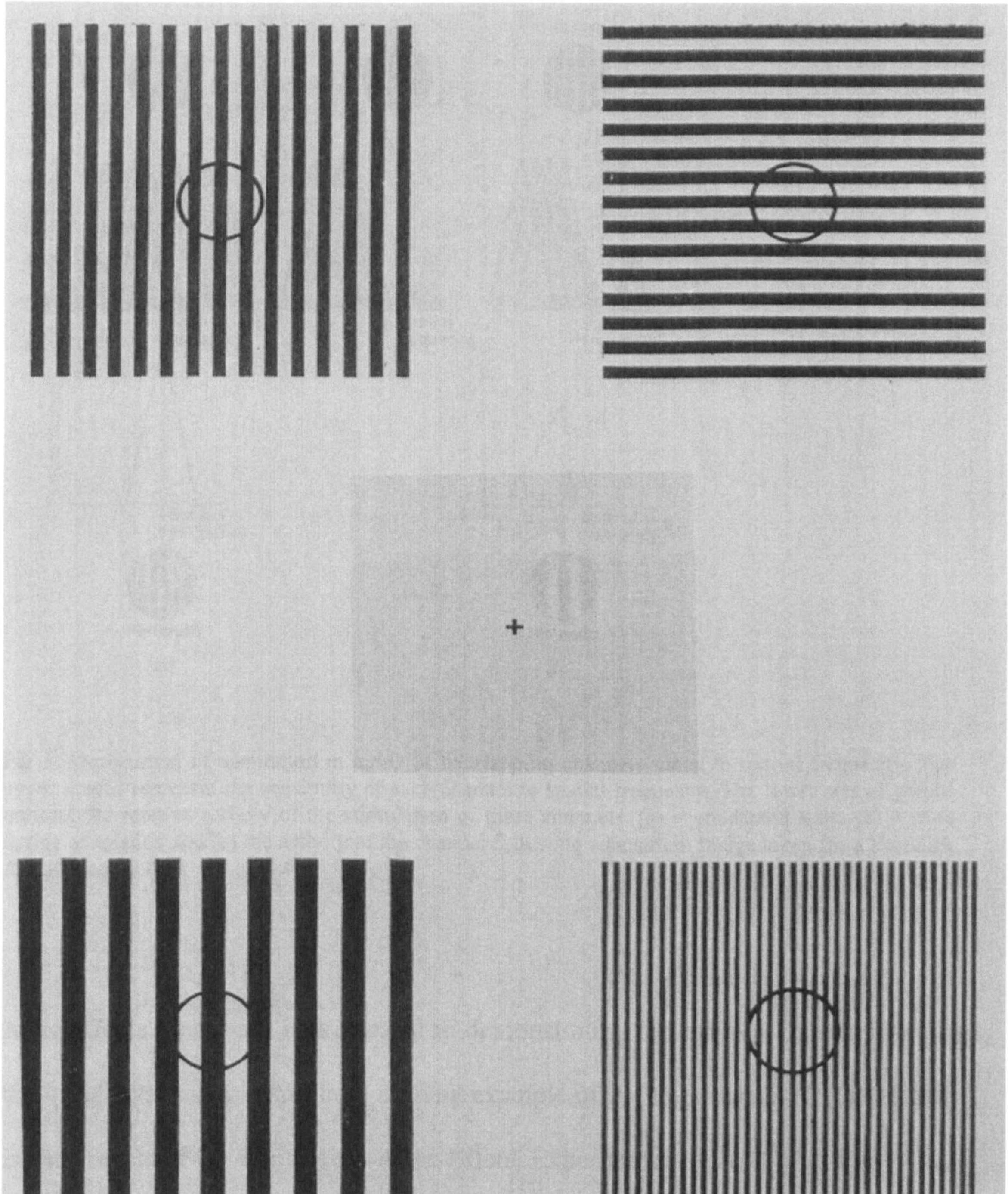

Fig. 2: Demonstration of selective adaptability of spatial frequency channels. If the circle within the top left grating is fixated for about a minute and then the central grating is looked at, the grating that is normally visible will first be invisible but will appear with time (5-10 sec). This effect does not occur when the other images are adapted too, demonstrating that the channel being adapted responds to a grating of the same orientation and spatial frequency. Image taken from Woodhouse & Barlow (1982).

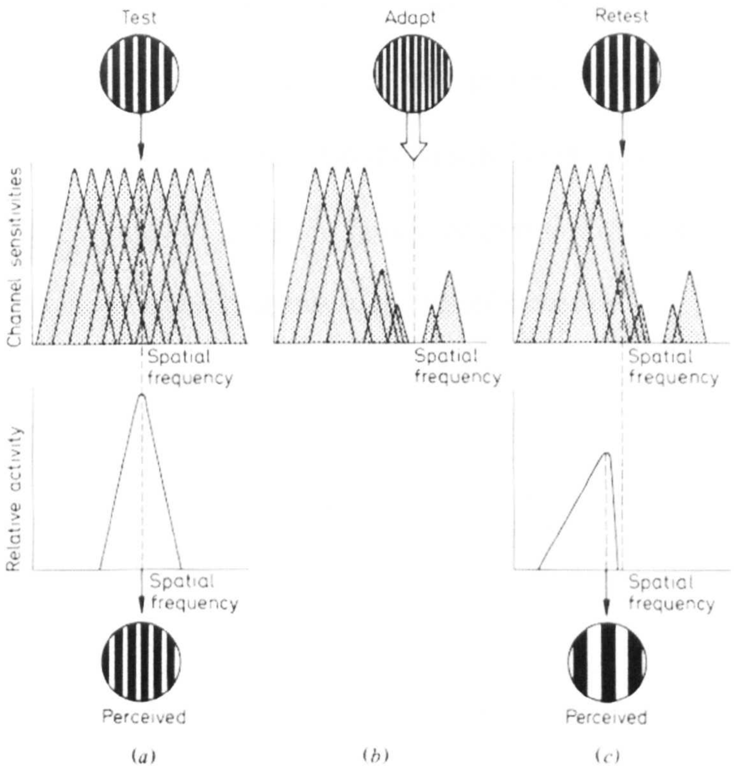

Fig 3: Explanation of adaptation in terms of overlapping channels tuned to spatial frequency. The upper graphs represent the sensitivity of each channel to spatial frequency. The lower sets of graphs indicate the relative activity of the stimulation of these channels. (a) = unadapted state, (b) = state during adaptation and (c) the activity of the channel following adaptation. Image taken from Braddick & Atkinson, (1982).

After-effects have been instrumental in demonstrating the nature of association in the visual system. An especially striking example of the importance of after-effects is that revealed by Contingent After-Effect Experiments (CAA) (see Fig. 4 for explanation). It should be stated that the after-effect state is not limited to visual perception and also occurs in the other senses such as in the auditory domain as well as in the vestibular after-effect. For example, Koenig and Dichgens (1981) examine the interaction of the after-effects to preceding vestibular and optokinetic stimulation. They report an after-effect in eye movements (after-nystagmus) in the opposite direction to preceeding vestibular and optokinetic stimulation. This effect was always stronger in the direction opposite to the vestibular induced adaptation. This led to the conclusion that the vestibular input has an increased input compared with optokinetic stimulation. This is an example of how cross-cue adaptation can be used to investigate processes in the visual system.

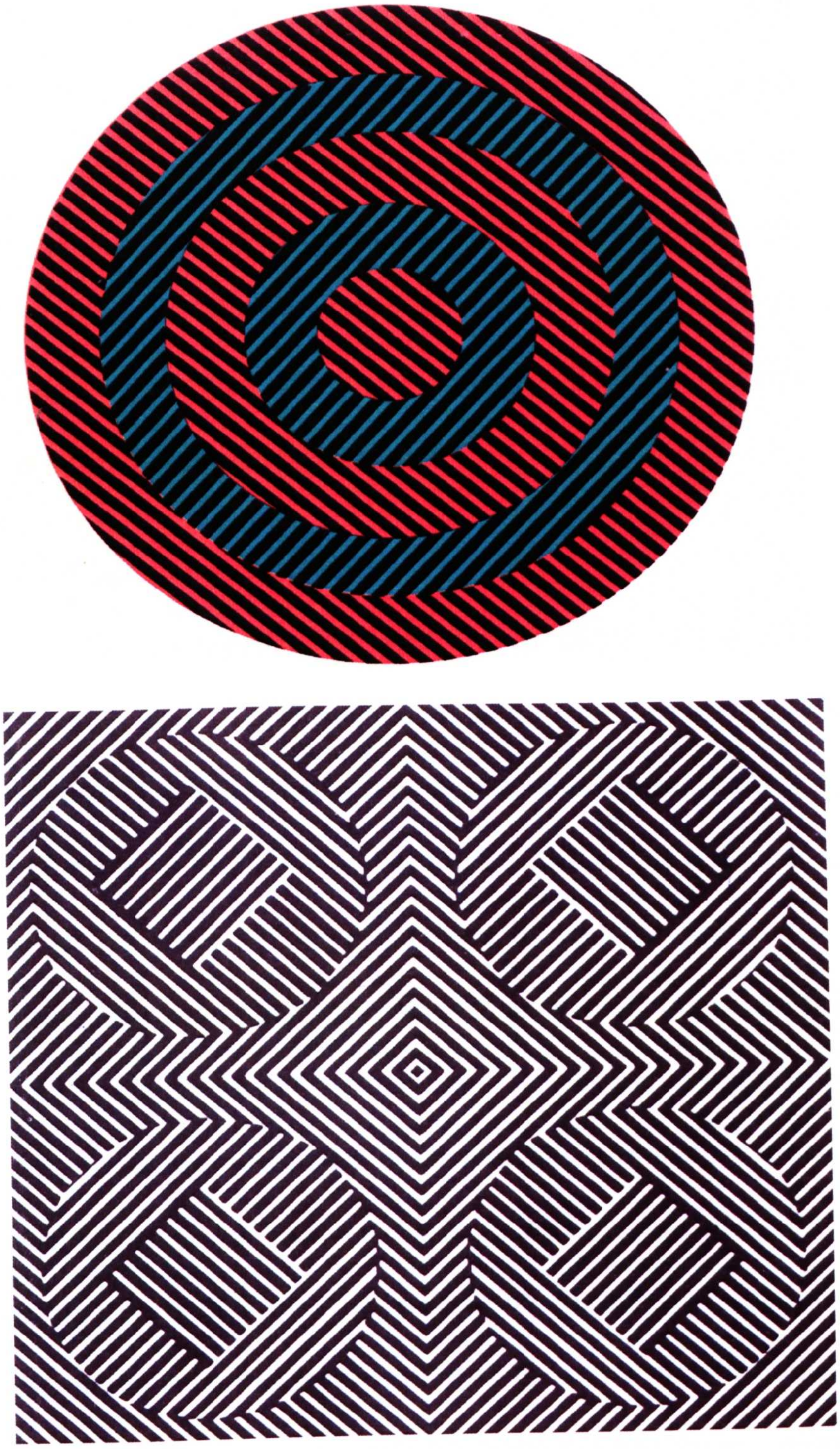

Fig 4: The McCollough Effect. After focusing on the colour image for a few minutes a strong after-effect can be observed when gaze is transferred to the black and white test pattern. The after-effect gives phantom colours that are paired to the orientation of the tilted lines. This is a contingent after-effect. Image taken from Mollon (1982).

2.2 Adaptation

The term adaptation can be applied in a variety of ways. Wade & Verstraten (2005) presented a classification for the description of adaptation. They described adaptation as a procedure, a process and a perception. The three terms correspond to the use of adaptation in experimental setup, the neural activity corresponding to the after-effects and the perception as what is experienced. To address the complex nature of adaptation this first section gives a brief description of the different contexts in which adaptation is used.

2.2.1 Adaptation as procedure

Adaptation as a *procedure* has proved useful in the investigation of visual processing. Following adaptation the subsequent changes in visual experience can be measured. This can allow inferences about mechanisms underlying visual processing to be made, as mentioned in Section 2.1 above. The technique relies on measuring the altered state following exposure to constant stimuli for a period of time. Theoretically, this stimulation leads to an alteration in neural firing rates compared to the unadapted state. Communication in cells can be represented in terms of firing rates, or action potentials. By continually stimulating a cell as is the case in adaptation, this will lead to a change in the firing rate of the cell as compared to the resting state of that cell. The presence of after-effects can be taken as evidence of a filter in the brain that is responding to the stimulation, and thus from manipulating the degree of similarity between the adaptation and the test, properties of the 'neural filter' can be inferred (Anstis et al, 1998). The filter is the underlying adaptation mechanism and is usually viewed in terms of channels. So, for example, when adapting to a particular velocity, subsequently viewed speeds that are slower than the adapting stimulus are affected, but speeds which are faster than the adapting stimulus are not affected. From this it could be inferred that the adaptation mechanisms in the brain, what is being referred to as filter here, is tuned to a range of velocities below the adaptation stimulus and not above.

Applying this logic has resulted in an abundance of knowledge and data concerning the different adaptation properties of the brain. Adaptation techniques have been used to illustrate the precise spatial tuning of disparity mechanisms (Long & Over, 1973) and have provided a basis for the difference between first- and second-order motion (Nishida & Sato, 1995). Further studies include adaptation to contrast, orientation, and curvature (Movshon and Lennie, 1979; Ohzawa et al., 1982; Carandini and Ferster, 1997; Carandini et al., 1997, Blakemore and Campbell, 1969; Hammond et al., 1989; Nelson, 1991; Blakemore & Over, 1972). Further studies include spatial frequency (Movshon and Lennie, 1979; Saul and Cynader, 1989), direction of motion (Maffei et al., 1973; Hammond et al., 1988) and velocity (Thompson, 1981).

The use of adaptation in these studies, and what they have been used to demonstrate about the visual system, is discussed in the following section.

Adaptation has been used to demonstrate pattern-selective mechanisms in visual cortical neurones. Movshon & Lennie (1979) recorded the activity of single neurones following adaptation to grating patterns, they demonstrate that sensitivity of a single neuron is reduced more to a specific grating compared with its sensitivity to other gratings. Critically, they showed that when the spatial frequency of the test and adapted pattern were varied the effect was not a uniform change in sensitivity. Instead, the effect of adaptation was specific to the spatial frequency of the test.

This was an important finding as it was previously thought that the effect of adaptation was to reduce the sensitivity of neurones uniformly to all stimuli. In essence, they demonstrate that the loss of sensitivity in neurones is specific to the relationship between the adapting grating and the test grating. This suggested the contribution of pattern selective mechanisms underlying adaptation and after-effects.

A further contribution in the understanding of the visual system can be seen by the examination of contrast adaptation by Ohzawa et al (1982). The key finding in this study is that the response amplitude and contrast threshold is extremely sensitive and is strongly influenced by the contrast levels the cell has experienced in the recent past. This highlights that adaptation is extremely sensitive to context.

Maffei et al (1973) examine contrast adaptation and report a value for the duration of the effect (30 sec). They also find that it transfers interocularly and that it is selective for orientation and spatial frequency. They did this by recording from a simple cell measuring responses to a grating drifting at the preferred orientation and direction of a cell. They demonstrate that in simple cells there is a recovery period in the neural response that is approximately 20 seconds to about 2 minutes, giving an average duration of about 30 seconds. They did not find the same time constants for complex cells. Their results are used to argue for similar neural correlates in response to adaptation in the cat as compared to the psychophysical data observed in humans.

In further studies using contrast adaptation, Carandini & Ferster (1997) examine the effect of contrast adaptation in the cat visual cortex. Through intracellular recordings they reveal that prolonged stimulation affects excitatory synaptic inputs that have input to cortical cells, rather than having a direct effect on the membrane potential of cortical cells or the membrane resistance. The largest observed effect was an effect of tonic hyperpolarization on the cells through contrast adaptation, which is the effect of adaptation on the absolute value of a cell's membrane potential. This finding is argued as evidence that the cellular mechanism underlying contrast adaptation is therefore caused by a decrease in the excitation received by a cell.

In a further examination of after-effects using orientation adaptation, Carandini et al (1997) report that responses were reduced in single cells following adaptation to a stimulus that contained two orientations, and *critically* one that was not optimal for the neuron under study. This demonstrated that some of the adaptation in the cells was specific to the contingency of two orientations present in the compound stimulus. Importantly, they also tested adaptation to contingencies involving spatial frequency. This however did not reveal the same pattern of effects as the orientation adaptation, and this has been used to argue there is differential adaptation in neurons to different types of contingencies. This finding could suggest that sensitivity to orientation contingencies in the environment is more prevalent than sensitivity of spatial frequency.

Adaptation has also been used to examine direction selectivity in striate cortical neurons. Hammond et al (1985) examined the response of striate cortical neurons to velocity and orientation in the cat. They demonstrate direction selectivity following adaptation of cells, in the opposite direction to the grating that was adapted too (in cells sensitive to direction).

These studies all demonstrate the application of adaptation as a tool for researching visual processing.

2.2.2 Adaptation as a Process

It has been suggested that the *process* of adaptation is what underpins the experiential change occurring in negative perceptions such as unpleasant odours and loud traffic (Barlow, 1997). Time lapses, the difference in time between exposure to the negative perception, often decrease the intensity of these experiences. The process is the vehicle by which the brain changes its response to the environment and can be understood as the neural or sensory change that occurs following prolonged exposure over a particular stimulus domain. This idea is supported physiologically by studies revealing an altered state in single visual neurons following exposure to a particular adaptation stimulus (Barlow & Hill, 1963; Giaschi, et al, 1993; Kohn & Movshon, 2004). As a process it is similar to the concept of habituation, which is a form of non-associative learning where there is a decrease in behavioural response following prolonged exposure to a stimulus. Adaptation as a process however may not necessarily involve learned suppression of a stimulus, but could be used to describe the underlying neural correlate of the change in the system.

2.2.3 Adaptation as a Perception

This change manifests itself as a change in *perception*. This change in perception is carried out through the process of adaptation, leading to an alteration of perception which then causes the presence of an after-effect. For example, if exposed to a particular attribute of the visual scene for a period of time a change in perception will occur which is termed an after-effect. An early example of this is referred to as "the Waterfall Effect", a phenomenon first reported by Addams at the Fall of Foyers in Scotland in 1834. Here it was discovered that after gazing at a waterfall for a period of time, the adjacent rocks appeared to move upward although in reality, of course, remaining stationary. This effect is more commonly referred to as the motion after-effect, a topic that has been thoroughly researched in the area of visual perception (Anstis et al, 1998).

2.2.4 Summary

In conclusion, after-effects are a historically important, striking visual phenomenon that have not only inspired people to search for an explanation but, in doing so, have provided a way to unlock some of the secrets underlying visual perception. The ways in which this has been done in many areas of visual perception is demonstrated in the examples of adaptation studies given in section 2.2.1. The different facets of adaptation have led to the creation of different classifications in order to clarify the exact meaning of the term in whichever context it is used.

2.3 Measurement of After-Effects

2.3.1 Overall Issues

Time course of after-effects

The time course of the process of adaptation appears to vary according to the type. The Motion After Effect (MAE) can occur over a short time scale and give rise to an after-effect (Kanai & Verstraten, 2005). However perceptual learning, involving discrimination can last over weeks and days (Haijing et al, 2006). Perceptual learning is an improvement in perceptual discrimination that occurs through practice. The practice hypothetically leads to a neural change which then impacts performance (Berardi & Fiorentini, 1981).

A common example of perceptual learning can be demonstrated after wearing prisms for a period of time. At first, the world appears distorted to the observer, but after a period of time the observer becomes able to respond so well that they can even catch objects that are thrown to them. After wearing the prisms for a period of time, the visuo-motor behaviour continues to be distorted. This is an example of perceptual learning that can occur through altering the relationship of the observer to the environment.

Another classic demonstration of perceptual learning is provided by Gibson & Gibson (1955) demonstrating that practice can improve visual discriminability of scribbled lines. This has been used to demonstrate how training can enhance category development, making the observer sensitive to information that was not previously available. This can be referred to as differentiation of whole stimuli (Goldstone, 1998).

Goldstone (1998) in a review of perceptual learning points out that perceptual learning does not exhibit good generality between tasks or different training situations, however it can occur cross modally. For instance, training in the discrimination of visual stimuli can be demonstrated to influence the tactile discrimination of the same shapes (Hughes et al, 1990). This highlights the similarity between perceptual learning and adaptation, as one of the key issues in adaptation as a process is the similarity between the test stimuli and adaptation.

Indeed, perceptual learning can be viewed as a type of adaptation. In the current research the focus has been on the adaptation occurring over a few seconds or minutes, as these provide strong effects and reveal the underlying plasticity of the brain in relation to our perception.

Interaction of adaptation and test

One of the major impediments to the accurate recording of a perceptual after-effect is the interaction of after-effect with the test stimulus during the measurement phase. Different results can be obtained with different test structures, making the underlying mechanisms of adaptation difficult to isolate.

For example, different MAEs can result from the same test pattern (Nishida & Sato, 1992; Wade et al, 1996, Wade & Salvano – Pardieu, 1998; Verstraten et al, 1999; van der Smagt et al 1999.) Using random dot kinematograms, Nishida & Sato (1992) demonstrate a positive MAE. However, other studies report a negative after-effect (the classic finding pertaining to the MAE) and highlight the sensitivity of the MAE to the test structure used (Verstraten et al, 1996). If a single mechanism is responsible for the MAE, it would seem logical to predict that the same MAE should be observed given the same test pattern. Instead, the results appear to be dependent on many factors, including the adaptation stimuli, the duration of adaptation and the task involved (Wade,1996).

This finding not only implies that the mechanisms underlying motion after-effect are complex, but that they may involve different neural sites. It also may point towards the contribution of the state of the observer when measuring the MAE (Culham et al, 1998).

The same motion adaptation can result in different after-effects given different global test structures. This demonstrates that the test stimulus is important and that more than a single process is being measured. It is slightly different in the case of the depth after-effect, where the interaction of adaptation and test has not been found to influence the magnitude of the depth after-effect (Taya, Sato & Nakamizo, 2005).

Prior experience

From prism adaptation experiments it can be argued that what can and cannot be adapted depends on the object-specific properties of the environment. An example of this comes from a prism adaptation experiment carried out by Kohler (1964). Here, on wearing optical distortion devices, it was reported that some objects were subject to inversion and some were not. There were objects that seemed resistant to the inversion produced by the prisms, whereas others were inverted. This is a curious finding and highlights that the role of prior experience is not uniform for all objects in the visual field, although this finding has been contested, (see Linden (1999)).

Stratton (1896) demonstrated no after-effect to prism wearing when the experiment was conducted indoors, but after-effects were reported when the experiment was conducted outdoors (1897c). This result highlights the importance of the observer's environment in the establishment of an after-effect.

2.3.2 Previous Methods

Different techniques have been applied when attempting to assess experiential changes occurring after adaptation. For example, in the first recorded experiments on after-effects, a verbal report that simply focused on the presence or absence of the effect was sufficient. With the introduction of more objective measures, this advanced to matching tasks. Here the participant was required to alter a probe along a particular stimulus dimension until it matched that of the perception. An example of a matching task employed in both motion and depth perception is of a key press. This means that observers pressed a key to mark when the depth appears to be equal to and in the same plane as the fixation stimulus (Rose, Hibbard & Bradshaw, 2003) and this has been carried out similarly for motion (Chadhuri, 1990; Nishida & Ashida, 2000). The most popular method has been applying duration in measuring the after-effect strength (Wade, 1994; Mather, 1998). It should be noted that duration is not synonymous with aftereffect strength despite being used most frequently as indicator of aftereffect strength. The assumption is that the longer the duration of the after-effect, the stronger the adaptation involved. However, there are reported difficulties with estimating the end of the effect (specifically beyond the usage of some nulling paradigm). As has been pointed out in Pantle (1998), p.39

" The cessation of an MAE is probably not returned to the state in which it was before adaptation, if the measurement is anything but instantaneous"

Another problem with these types of measurement, however, is the re-adaptation or recalibration to the test stimulus, giving an inaccurate measurement of the underlying after-effect.

Using duration as a measure of the after-effect is also problematic because it does not give an indication of the strength of the effect and how it changes over time. Using a nulling technique, in which the after-effect is counteracted or nulled by a test stimulus that normally provides the opposite percept, gives a more direct indication of the strength of an after-effect. A significant contribution to this field is the study by Castet, Keeble & Verstraten (2002). In attempting to measure the motion after-effect, they introduced a nulling paradigm in which the overall energy of a dynamic random-dot stimulus is maintained the same, but the proportion of coherently moving -moving with the same global direction- dots can be changed. A dynamic random dot stimulus is a display containing moving elements (dots) positioned at random on the stimulus. It can often appear as twinkling to the observer. The proportion of dots required to null the after-effect is given as the strength of the after-effect.

However, when looking at the problem of measurement of visual after-effects it would be useful to capture their full temporal dynamics (i.e. strength, duration and how that strength changes over time). Measuring the temporal dynamics of after-effects is also important from the point of view that theories concerning the nature of after-effects are changing. If adaptation is explained in terms of neural fatigue

(Sutherland, 1961), then the temporal characteristics of the decay of the after-effect should be predicted by physiological recordings. If adaptation is reflecting underlying neural recalibration and is responsible for efficient information transmission (e,g as proposed by Wainright, 1999) then the changing temporal characteristics of the after-effect could affect the changing sensistivity to the environment and signal transmission. When trying to understand the neural mechanisms underlying adaptation, then it is important to have a method of how the after-effect is changing in time.

Furthermore, given the change of the theory to a dynamic system that is recalibrating over time, obtrusiveness of measurement becomes a particular problem. When the system was seen as passive this was not such an important issue.

Newer theories of adaptation are concerned with the idea that the perceptual system is recalibrating and that the functional significance of adaptation is to provide constant plasticity of the perceptual system in reacting to a constantly changing environment.

Consequently, we wish to propose a method of measuring the after-effect that captures both the duration and change in magnitude over time. We do this by measuring the change in perception whilst nulling the after-effect with different tests. This has the advantage of giving the full temporal dynamic of the after-effect.

2.4 Theoretical Explanations of Adaptation and After-Effects

Despite the wealth of data surrounding the phenomena of adaptation, the theoretical framework to understand the process remains to be developed more fully. A number of explanations of adaptation have been proposed, with earlier explanations relying on the fatigue of visual neurons known as 'ratio models' (Sutherland, 1961; Barlow & Hill, 1963) and later ones relying more on distribution shifts in a neuronal population response (e.g. Mather, 1980). However, the exact neural processes involved remains unclear.

As mentioned previously, during adaptation it could be that 'channels' representing broad groups of neurones tuned to particular visual attributes, such as spatial frequency, have a change in profile due to adaptation (see Fig.3). Following adaptation, when the same channel is stimulated there is a change in perception, and an after-effect is perceived. The underlying mechanism that is proposed is often that of neural fatigue. In particular, the nulling technique has allowed the inference of properties of visual after-effects, which has in turn led to the generation of theories concerning the adaptation process in the visual system. The results of this work have contributed to the view of the after-effect as a recovery period of a pool of neurons back to an initial pre-adaptation state (Pantle, 1998). This can be termed the 'fatigue' theory of adaptation (Howard & Rogers, 2002). This theory is particularly prevalent in the research concerning the motion after-effect (MAE). The assumption is that there is one common underlying adaptation process responsible for the effect. Given adaptation to a single component stimulus moving in one direction it was thought that the responsiveness of a pool of directionally selective neurons was changed, leading to an imbalance when presented with a similar stimulus and resulting in the after-effect. This theory predicts that the properties of the after-effect would simply change as a result of the return of this hypothetical group of neurons to their previous constant state (Pantle, 1998). Many of the experiments reflect this assumption (Verstraten, 1996).

The central idea is that there are neurones responsible for coding direction of motion that are paired. When one of these is stimulated to a greater or less extent than the other neuron that it is coding for, there is a resultant imbalance and a subsequent perception of motion is perceived when no motion is present. Sutherland (1961) is the key paper that proposes this theory and the Barlow & Hill (1963) paper presents recordings from motion sensitive cells in the rabbit giving convincing electro-physiological support to this theory.

However, this theory has been challenged particularly in the motion literature by the finding that the MAE obtained for transparent motion is uni-directional (Verstraten, 1994). This presents a particular problem for the ratio-models. An after-effect moving in two directions is expected as a prediction from the ratio encoding explanations. Instead, what has been observed is an after-effect that is the vector sum of the two adapting components (Mather & Moulden, 1980).

This finding has significantly impacted the underlying theory regarding the explanations of after-effects. The ratio model has been altered to contain tuning to many different directions of motion (rather than just opposite) and the distribution shift model has been proposed by Mather (1980). This model can account for the presence of a uni-directional after-effect following adaptation to two directions of motion. The critical difference in this model from the previous models is that the activity of all detectors tuned to all directions is taken into account, as opposed to the output of motion sensitive pairs tuned to opposite directions, as was previously proposed in the 1960's.

The critical underlying mechanism in these theories is the fatigue of neurons leading to an imbalance in the perception of motion. However, previous work on adaptation in other areas does not suggest that this is the case. The magnitude of the after-effect can be increased given a delay between the adaptation and test (Spigel, 1963; Keck & Pentz, 1977). Using the 'fatigue' theory of adaptation, this only makes sense if the delay is somehow stopping the rate of decay of the response of the neurons. Keck & Pentz (1977) argue that different balanced states underlie the dynamics of the after-effect due to the finding of a non-linear relationship between test contrast and speed/magnitude of after-effect. They found that the dynamic of the after-effect completely changed with changes in test contrast. This included a change in both the initial speed and duration. This led to the conclusion that after-effects may be the result of adaptation occurring at a number of different points in the visual system as opposed to being the result of the modification of one underlying process, a view that was previously assumed. A change in test contrast causing a change in the temporal dynamics of the after-effect suggests a change in the underlying channel that is being stimulated during the testing phase, relating what is being viewed in the test to what has been viewed during adaptation. This idea that after-effects are the result of multiple adaptive responses in the visual system is also supported by physiological findings.

A movement towards the idea of multiple adaptive responses underlying adaptation is also consistent with more recent findings investigating the depth after-effect. The particular dynamics of the after-effect occurring in depth has been found to be dependent on the properties of the test stimulus. These findings have since been supported (Long & Over, 1973; Mitchell & Baker, 1973; Graham & Rogers, 1982a; Rose & Price, 1995) suggesting that the adaptation process is not as simple as the fatigue theory would suggest.

One of the major problems for the fatigue account of adaptation includes the fact that there is storage of the effect (Spigel, 1962a). This means that when there is a delay between the adaptation and test, a period in time when the neurons response could recover from fatigue, an after-effect is still observed. This has also been shown to occur not only for blank test intervals but also when different patterns are presented in between adaptation and test (Thompson & Wright, 1994b). Neural satiation or fatigue does not account for this finding, and thus the storage effect is used to argue against the fatigue hypothesis of adaptation. However, one finding that is clear is that despite storage of the effect, this storage is not perfect (Weisenfelder & Blake, 1992). This can be used to argue that there is neural decay occurring during the intervening time period following adaptation.

Other theories that can account for the presence of phenomena such as the storage effect include those of error correction, optimal encoding and recalibration. These are presented together as they are theories that do not necessarily exclude one another, and thus elements of each may be operating at the same time (Mather & Harris, 1998). Indeed, functional accounts of adaptation have been split into main categories by Mather & Harris, (1998). This distinction is used in brief presentation of these theories in the following section.

Error Correction

In this theory there is an assumption about the likely occurrence of a stimulus in the world, like a norm, which is representative of any range of a stimulus domain (Howard & Rogers, 1995). An after-effect is the perceptual consequence of the system trying to return to this norm, but the perception is erroneous due to the prolonged stimulation. This theory posits that the visual system is sampling the incoming information over time and there is a comparison of actual and time-averaged activity. However, one of the main problems regarding this theory is that it does not account for the adaptation and consequent after-effects that can be observed even following brief exposure times. In an attempt to incorporate this finding, the following theories have been more recently developed.

Optimal encoding & Recalibration

More recent attempts at theoretical explanations of adaptation and after-effects have focused on issues such as optimal encoding (Wainright, 1999) and cue recruitment (Haijiang, Saunders, Stone & Backus, 2006). The fundamental difference in these approaches is the contrast between learning and encoding of information. In one approach the statistics of the natural image are utilised and encoded by the visual system, giving a picture of the visual system that is dynamically altering in response to the environment (Wainright, 1999). Other approaches see the adaptation process as a form of classical conditioning, highlighting the role of experience in perception (Haijang, Saunders, Stone & Backus, 2006). These accounts view the functional role of adaptation as a mechanism that is used by the perceptual system to enhance the processing of information, which stands in direct contrast to the idea of the neural fatigue hypothesis. The emerging theoretical picture of the visual system as constantly recalibrating itself and not being as passive as once suggested is relatively new in the theoretical understanding of after-effects. However, the reliance of perceptual systems on constant input has been demonstrated by the fact that in the absence of stimulation, people will begin to hallucinate and experience sensations in the visual and auditory domain, an example being sensory deprivation research (Zubek, 1966). This is also known to be true in body movement, which shows an initial adaptation effect during the first three hours of sensory deprivation followed by an increase to a maximum at 12 hours (Zuckerman et al, 1966). This indicates that the system is at least expecting a variable sensory input. It may be possible then, that the adaptation process provides the key to understanding the relationship between this constant input and perceptual experience. Given that adaptation occurs and is important within the visual system it is scientifically important to attempt to measure this. The need for this has been highlighted by Wade & Verstraten (2005) p. 97:

“With the acceptance that a phenomenon can be considered as adaptation some method of accurately assessing it is required. This is the procedural phase. It is essential in terms of deriving reliable indices of the perceptual change”.

The following section, therefore, focuses on the techniques applied to the measurement of after-effects.

2.5 Overview of the proposed technique

In summary thus far, adaptation can be used as a tool for investigating properties of the visual system. This has not only contributed to the knowledge of the particular characteristics of after-effects but has led to the generation of theories concerning the underlying mechanisms that are responsible for the observed phenomenon. The ‘fatigue’ theory of adaptation has been replaced by a view of multiple encoding of adaptation information, which is consistent with more recent studies in the area. This has led to the search for new theories to account for the complex and varied adaptation properties that exist. Current theories attempt to understand the process through coding of natural statistics and learning in the environment, however no clear model exists to account for the phenomena. Chapters 3, 4 and 5 of this thesis focus on the application of a technique for deriving the temporal dynamics of after-effects. The following section presents a broad overview of the technique and lists the benefits of its application in the measurement of after-effects.

2.5.1 Related attempts at measurement

A key paper in previous studies addressing the temporal dynamics of after-effects was that of Hershenson (1989). The technique developed in the present research is most similar in spirit to this paper and therefore the findings of this paper are discussed here. Hershenson (1989) aimed at monitoring the time course of the decay of the motion after-effect. The importance of this paper was that duration and time constant had been assumed to be independent of inspection duration and could be used to characterise the underlying structures that mediate the MAE. In this paper, through monitoring the temporal properties of the after-effect, it was demonstrated that the after-effect duration was a function of the inspection duration.

The study consisted of two experiments, both looking at the effect of inspection duration on the perception of the motion after-effect as measured with a static test. Participants adapted to upward motion. The adaptation stimulus was horizontally striped illuminated paper. In the first experiment the inspection duration was varied between 30 sec and 900 sec. In the second experiment the inspection duration was varied between 20 sec and 120 sec. The method used to quantify the after-effect was to monitor the perception of the motion after-effect through verbal report. Using an

11-point rating scale, participants called out their perception of the after-effect. The strength of the effect was given between the number 10 and 1. Testing was stopped when two '1''s were called out in succession. Using a metronome and recording on a tape, these responses were sampled every second and then coded to give a picture of the dynamics of the after-effect.

After obtaining these results for both these experiments, Hershenson (1989) described three different stages to the motion after-effect; an initial maximum strength stage, a decay stage and a tail stage. Looking at these temporal properties led to the discovery that the inspection duration determined the length of the after-effect and that there was a square-root law dependence of after-effect duration on inspection duration.

The technique presented in the following chapters is also an attempt to monitor the temporal dynamics of after-effects. It is similar to the work of Hershenson (1989) but differs in precisely 3 important ways: (i) it uses forced-choice methodology (ii) it uses the method of constant stimuli and (iii) the test stimulus can be varied. Furthermore, using this method allows an estimate of the relationship between the after-effect strength at time zero, and is not entirely a relative measurement between consciously experienced perceptions.

2.5.2 Relation of present technique to broad range of techniques utilised in investigation of after-effects

In measuring an after-effect the type of task that is employed could be a factor in accurately measuring its magnitude and temporal variation. Indeed, it has been argued that this may be the reason for the differential reports of after-effect strength[1] and duration obtained in different experiments (Pantle, 1998).

Two techniques employed frequently in the investigation of after-effect strength are that of matching and nulling. This following section is concerned with a discussion of matching and nulling tasks and how they can be used in obtaining a measurement of an after-effect. Examples from previous research are given to illustrate the differences in the two types of tasks. It is concluded that the techniques are in essence very similar: the main difference being in one the task is a comparison judgment and in the other a cancelling out procedure is used. One important consequence of this difference may be that when implementing a matching task the comparison stimulus is present throughout the testing period. This may cause a different result from having only the test stimulus present (as in a nulling task), as stimulus context and history are important in the perception of after-effects.

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[1] For the present section after-effect 'strength' is the term used when describing some measurement techniques, but this is ambiguous. This can mean two things- it could be the after-effect in terms of duration (time- how long the effect persists), or in terms of magnitude (the size of the alteration in percept caused by adaptation). Due to the fact that both techniques discussed here (matching & nulling) can be used to access both aspects of the after-effect, the term strength is used and it is intended to encapture the entire after-effect in both terms of magnitude and duration.

Nevertheless, it is concluded that the information extracted using these techniques is very similar. This arises because in both cases the value underpinning the measurement of the after-effect is reliant on the point at which the after-effect is no more, which is calculated in most cases via the value introduced into the comparison or nulling parameter. The relation of the present technique to matching and nulling tasks is discussed.

Overview of Matching and Nulling Techniques

One definition of matching is to 'make something identical to' that can be contrasted with nulling 'to reduce something to no importance' (www.dict.die.net). In the context of measuring after-effects, both approaches have been utilised. When carrying out a matching task the observer must make a decision concerning the test stimulus in comparison to another stimulus. An example of this is present in research investigating the velocity after-effect, where the strength of the after-effect can be inferred by asking observers to match the speed of a test stimulus with that which is occurring following adaptation to a particular velocity. In this way, an estimate of the speed of the after-effect being experienced by the observer can be obtained. In using this task there is always a standard and a comparison with which the observer must make a decision. The essence of this judgment is a comparison of the observers' perception with that presented in the test. By varying properties of the comparison, thresholds can be calculated concerning the strength and variation of the perception of the after-effect. Indeed, this is the technique employed by the papers measuring the velocity after-effect in a later section of this review (for instance see Bex et al, 1999).

In contrast, a nulling technique attempts to access the strength of the after-effect via direct cancellation of the after-effect, usually achieved through presenting percentages of the adaptation stimulus in the recovery period following adaptation. From the amount of energy (dependent on the stimulus dimension) added in, the magnitude of the after-effect can be inferred. The amount required to cancel (null) the perception of an after-effect is then used to give an estimate of the strength of the after-effect. An example of a nulling technique that has been used to infer the magnitude of the depth after-effect is that used by Blakemore & Julesz (1971). From adapting to +/- 2 arcmin disparity, they found an introduction of 30 arcsec was required to null the perception of the after-effect present following adaptation. The value added in to cancel the after-effect was then taken as a measure of the after-effect strength. This differs from a matching task where a comparison is made and properties of the comparison are varied (usually using an adaptive procedure) aiming to converge on a point where the after-effect and test are in balance. From the properties of the comparison used, the strength of the after-effect is inferred.

As a direct measure of an after-effect, there are reasons for using both methods. A problem faced by using matching techniques when trying to extract the temporal characteristics of the decay of the after-effect is that the presence of the match may have an influence on the after-effect itself. Furthermore, if the match is continually varying in relation to the test, this provides a continually changing context for the after-effect. If trying to map the decay of the after-effect without this interaction, inferring properties of the after-effect from a comparison judgment may influence the act of measurement itself.

For this reason, in some cases it may be better to apply a nulling technique. This is because in the matching task the observer is being asked to make a comparison about the present stimulus and the after-effect strength which is being inferred from this. When using a null test method the observer is addressing the appearance of the test as it appears at that present moment. How this judgment changes as a function of the energy in the test is used to infer the magnitude of the after-effect. This approach also is problematic because the act of nulling itself could affect the temporal characteristics of the after-effect, which presents a similar problem to that encountered when making a comparison in a matching task. Due to the subjective nature of after-effects. it is likely that any change in the stimulus will alter the temporal characteristics of the after-effect. Therefore, using nulling paradigms as a method of investigating after-effects presents difficulties also.

Further examples of Matching & Nulling Tasks

Graham & Rogers (1985) report an after-effect strength of 85% for measuring the depth after-effect. In their experiment they adapted observers to corrugated gratings, and had them make eye movements across this grating for a period of time. To measure the after-effect produced by this adaptation, they had observers add in disparity to a corrugated grating until it appeared flat. They found that about 85% of the disparity in the adaptation stimulus was required in order to make a subsequently viewed stimulus (which actually was flat) *appear* flat. This is what led to the conclusion that they had an after-effect strength of 85% in their experiment. This is an example of using a nulling technique to infer the strength of an after-effect. The inference is that the value obtained is dependent on the perceptual change required to make the after-effect disappear. If viewing adaptation in terms of recalibration, it is the amount of energy required in order to recalibrate the system. The value obtained using this method is dependent on the length of time of adaptation and whether top up procedures are used (Howard & Rogers, 2002).

In contrast, Bex et al (1999) access a measure of the velocity after-effect using a matching technique. Measuring at multiple points both during and following adaptation, they report an after-effect strength for the velocity after-effect that was a value that was dependent on the speed used during the adaptation and test period. The value obtained for the perception of the velocity at any point in time was determined by the amount of speed present in the test. By correlating the amount of velocity in the test stimulus at the point of subjective equality, a measure of the strength of the after-effect was obtained for many different time intervals. Again, the values obtained are dependent on the length of time of adaptation and whether top up procedures are used.

Summary

Both techniques aim to extract similar information: how much of the adaptation stimulus is required to cancel the influence of the after-effect built up during adaptation. In both techniques, the amount of the adaptation stimulus strength that is required to make the after-effect disappear is the value which is taken as the strength of the after-effect. This can be sampled over time and a full picture of the strength and time course of the after-effect obtained. The following section highlights the similarities between these techniques in measuring after-effects, any differences that may arise due to the technique applied and the difference between the present work and previous investigation of the temporal aspects of adaptation.

Current technique

The technique employed in the first three chapters of this thesis seeks to capture the temporal dynamics of the depth and the motion after-effect. The technique we use is a variation of a nulling technique. It is not identical to the normal usage of a nulling paradigm, because the nulling is not controlled or manipulated in any way by the observer. The test stimulus does vary in the amount of the adaptation stimulus present in the recovery period. The observer is asked the same question about the appearance of the test stimulus at every time interval. To make this into a matching task, a stimulus the same as the adaptations stimulus would be placed next to the test and the observer would make a comparative judgement. This would be impossible to do using the present technique because it relies on the time taken for the perception of the test stimulus to reverse (it relies on the adaptation causing a perceptual reversal of the stimulus in the direction of the after-effect). By presenting the adaptation stimulus at the same time this would immediately null the after-effect and not allow an estimate of the magnitude of the after-effect.

In summary, matching and nulling techniques have both been used extensively to investigate the perception of after-effects. A subtle difference lies in the task required by the observer. In a matching technique there is a comparison, with simultaneous presentation of a test. When using a nulling technique, the observer is required usually to change aspects of the stimulus to cancel the after-effect. A theoretical issue is that when attempting to measure the temporal dynamics of after-effects, when making a judgment (is this faster/slower for example, as is required in a matching task) accessing the after-effect through a nulling approach may be more direct because a question is being asked about the appearance of the stimulus at that present moment to the observer. However, a nulling paradigm is also problematic when attempting to access the changing characteristics of an after-effect because the act of nulling itself could affect the temporal characteristics of the after-effect. We have adopted a variation of a nulling technique that aims to keep interaction of test and adaptor to a minimum.

Techniques in measuring after-effects: Velocity After-Effect

One aim of the present work was to develop a technique that could quantify the temporal dynamics of after-effects. This method employs a nulling technique over time in order to access the magnitude and duration of the after-effect. Another approach that could be used is a matching technique. Utilising a matching technique has proved difficult as regards investigation of the Motion After Effect (MAE) because the matching motion necessarily involves a change in motion over time (whereas the MAE does not) and the speed of the MAE is typically slow (Pantle, 1998). This may have resulted in an avoidance of matching techniques in the research concerning after-effects due to the MAE being the most thoroughly examined after-effect by far.

However, this problem is not the same when investigating the temporal dynamics of velocity after-effects. The velocity after-effect (VAE) is the reduction in perceived speed as a consequence of adaptation to motion moving at a particular velocity. The following section presents the methods conducted in three specific papers that have explicitly examined temporal characteristics of the velocity after-effect. These papers are Bex, Bedingham & Hammett (1999), Clifford & Langley (1996) & Hammett, Thompson & Bedingham (2000). This is done to illustrate the techniques that have already been applied in the investigation of temporal dynamics of after-effects. The differences used in the current approach are then outlined. A commonality to the methods employed in these papers is that of a matching technique to establish the change in velocity perception. This method is first focused on, using the Bex et al (1999) paper so as to illustrate a direct comparison with the current technique utilised in the present examination of after-effects. Following this, the exact methods used in each paper are discussed.

Bex, Bedingham & Hammett (1999)

Of relevance to the present research is the technique that was used to measure the VAE developed by Bex, Bedingham & Hammett (1999). In this research they pursued an examination of the velocity after-effect. As has been mentioned in other sections, the velocity after-effect constitutes the change in perception that occurs when there is a decrease in velocity following prolonged exposure to a stimulus moving at a particular velocity (Thompson, 1976). However, they also examined other aspects of the VAE, including the effect of contrast, and varying contrast together with velocity. The technique remained the same in each of these experiments, demonstrating that with regards to the VAE, this matching procedure can be used as a method for examining the characteristics of the after-effect. The exact procedure implemented is highlighted in the following section.

Their approach begins by asking observers to make a velocity judgement (which stimulus appears faster?) at small time intervals throughout the adaptation period and recovery. By using an adaptive procedure, they varied the stimulus parameters until the match appears the same as the standard on 50% of the trials. From carrying this out repeatedly, a psychometric curve for the perception of the after-effect (along one dimension) could be built up. This was carried out for each time interval, yielding a psychometric curve at each of these time intervals. From this, the curves were fitted with an exponential function and the 50% point on the curve extracted. This gives an estimate of the speed of the moving grating at each time interval. This can be done for each time interval throughout the adaptation and recovery period, giving a picture of the temporal dynamics of the VAE. In this technique, the magnitude of the after-effect is the speed of the match (the 50% point on all the curves) and the time constant is the collection of the extracted perceived speed match correlated with the time interval it was obtained at and fitted with an exponential function.

The exact results obtained by Bex et al (1999) are illustrated in Figure 5.

Procedure

This specifically involved asking observers to match the velocity of a sinusoidal grating to that of a standard which was presented repeatedly through the adaptation and recovery periods. In doing so, they sampled the perception of the velocity characteristics throughout the adaptation and recovery period. This is useful because in trying to ascertain the functional significance of the after-effect, it is essential to know the changing characteristics during adaptation and recovery. Thus, they sample the changing characteristics over time of the velocity after-effect which is what the present research attempts to do in relation to the motion after-effect and the depth after-effect.

Specifically, they examined the VAE present after exposure to horizontal sinusoidal gratings which were (2 cyc per deg) drifting within stationary Gaussian windows. These were then centred at 2 deg to the left or right of a black fixation cross. During an adaptation period of 30 seconds the adapting pattern was continuously present. The match pattern was presented every 3 seconds throughout this first thirty seconds. Following this 30 seconds, the adapting pattern was then presented for 1 second every 3 seconds throughout the recovery period. The match pattern was presented every 3 sec for 1 sec throughout the adaptation and recovery periods. The crucial difference therefore temporally is that there was a continuous adaptation pattern present during the adaptation phase and this then changes to intermittent during the recovery phase, where both the match and adaptation are present. The temporal frequency, location and direction of motion were randomised across sessions. Using an adaptive procedure (QUEST) observers were asked to judge which was moving faster (which interval). 20 independent staircases were used, one for every test interval. This was used to build 20 psychometric functions for 3-second test intervals throughout each run.

The results of this experiment were that the apparent speed of the adapting pattern slowed exponentially during adaptation with a time constant of approximately 5-6s. The recovery time was found to be slower (9-29 sec). Their measure of after-effect strength (referred to as attenuation, was greater at the faster speed employed (15hz) where the apparent speed fell to 44% of the adapted speed. In the slower speed used (8hz) the apparent speed fell to 57% of unadapted levels.

Comparison with present technique

One of the aims of the present research was to derive a method of measuring the temporal dynamics of after-effects. In particular, we wished to use a method that would give both an estimate of the time constant of the after-effect and also its magnitude. The technique utilised by Bex et al offers a method of doing this. Using their approach gives an estimate of the perceived speed at each time interval both in the adaptation and test, which can be recorded and used to estimate an overall time constant for the change in sensitivity to speed. Using this method, the time constant is derived by extracting the match speed and at each test interval and then fitting this with an exponential function (in this case an exponential decay function). The magnitude of the after-effect is therefore the perceived speed at each time interval and the time constant is the decay in this perceived speed once correlated with time.

This differs from the technique we employed in the present research. The current method presented obtains an estimate of the magnitude of the after-effect by asking observers about the appearance of the stimulus whilst varying amounts of the adapting stimulus is presented. It is similar to a nulling technique. By varying the amount of nulling in the recovery period, the time constant of the decay is predicted to change. So for example, one prediction could be that a stronger stimulus (i.e. one that is most similar to the adaptor) causes a rapid decline in the perception of the after-effect[2]. The decrease in this time constant with varying levels of the adaptation stimulus present in the recovery period is then used to calculate the temporal dynamics of the decay of the after-effect. The magnitude of the after-effect at any point is the proportion of times the stimulus (in the recovery period) is viewed in the direction of the after-effect and the time constant is the time to reach the PSE (the point at which the stimulus is no equally perceived in the direction of the after-effect and the adaptor). This estimate is gathered for a number of different percentages of adaptor (which could be said to represent different nulling strengths) and this used to give the overall picture of the temporal dynamics of the after-effect.

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[2] This assumes that recovery is determined by magnitude of adaptation. Although related, other factors have been found to influence dynamics of recovery (Hammett, Thompson & Bedingham, 2000). This is a point discussed in a later section. The only important point is that there is some relationship between the time course of the after-effect and the nulling value used in the testing period.

Specifically, the procedure employed in the present research differs from the procedure implemented by Bex et al (1999) in the following ways shown Table 1:

Table 1. Table to illustrate the differences between the current technique and that applying a matching task. Bex et al (1999) is given as an example.

Paper	**Bex et al (1999)**	**Present Technique**
Task	Matching Task	Variation of a nulling task
Methodology	Adaptive procedure	Method of constant stimuli
Time Period	3 sec interval throughout	No measurement during adaptation, then random 2 sec throughout
Analysis	PSE extracted from convergence point obtained through matching	PSE extracted from time taken to reach null point of after-effect and test

The reasons for these differences are discussed in the following section.

Task

There is an important difference in the task used when interested in the temporal dynamics of after-effects. This difference in technique may highlight the difference in motivation between the procedure implemented by Bex et al (1999) and that utilised here. Bex et al were first of all interested in the changes in speed sensitivity both during and following adaptation. To do this the adaptation stimulus was continually present for the first 30 seconds and then present intermittently during the recovery period. This means that adaptation decay could be prohibited during the recovery period. Consequently, it could be argued that the normal decay function (following cessation of adaptation) is not measurable in this case. In the present research we were interested in measuring this change following adaptation, so we did not want the adaptor present during the recovery period. It was a critical aim that the adaptation and test be different so that the after-effect could be 'superimposed' in a sense on the test used during the recovery period.

Method

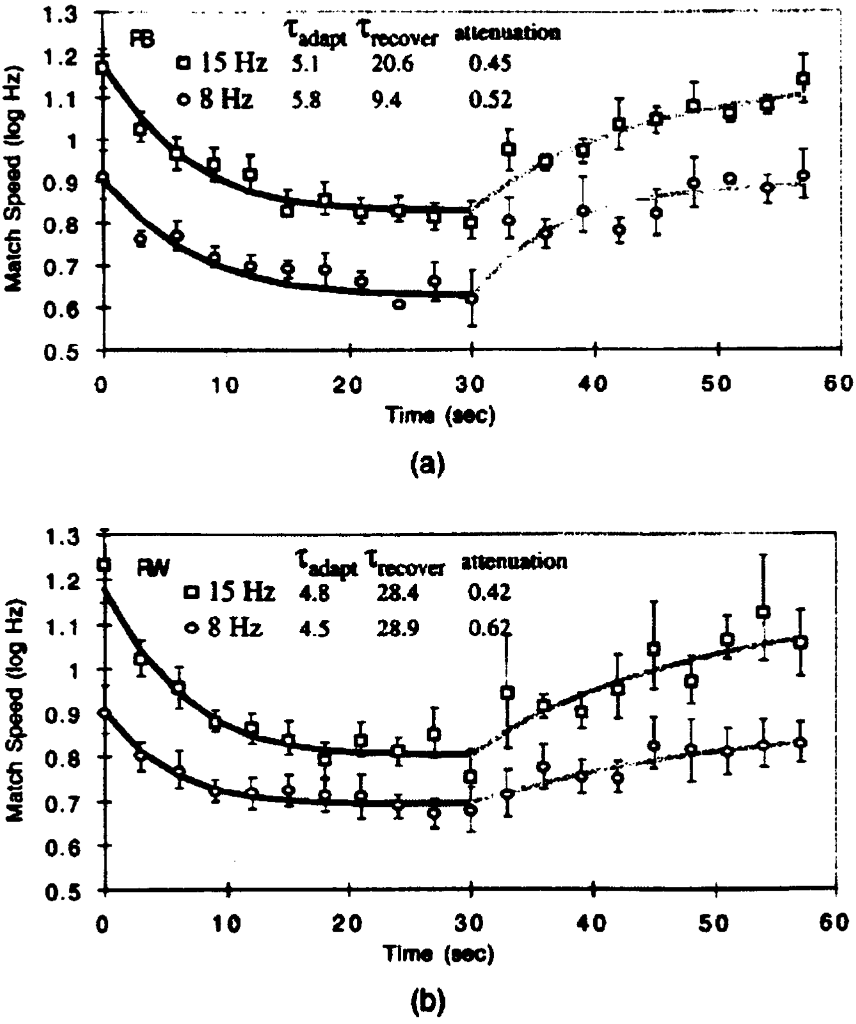
Bex et al (1999) employ an adaptive procedure when estimating the magnitude of the after-effect at each time interval. In the present research we utilise the method of constant stimuli. By using an adaptive procedure this means that the strength of the comparison test used by Bex et al would vary from trial to trial in order. In the testing period in the present research the strength of the test was kept constant throughout the testing period. The motivation for this is that when wishing to extract the change in the magnitude of the after-effect with time, we wished to build up a picture of the decay for each strength of adaptor used in the recovery period. If an adaptive procedure was utilised, different strengths would be present at each time interval in a different order each time. This could influence the perception of the after-effect between different time intervals and not lead to a build up of a picture of the decay of the after-effect throughout the testing period. Within each time interval it means that nulling effectively would be taking place in the procedure used by Bex et al, and the magnitude of the after-effect is derived from this. However, this gives a random sequence of speeds used throughout the time interval, which could affect the magnitude of the after-effect. If wishing to extract the temporal dynamics, this could be important. In conditions where adaptation has ceased and the aim is to measure the dynamics of the recovery, this measure will not only be affected by the presence of the adaptor, but also by the sequence of the match that appears on each test trial. For the specific aim of the present research we therefore chose to use a continuously present test with the aim being to titrate the after-effect and its variation with time, employing a variation of a nulling procedure (a variation because the observer did not adjust the test stimulus). A critical difference that may be of importance in the measurement of after-effects is that in the present study the adaptation stimulus was never present in the recovery period. However, in the study by Bex et al the speed present in the adaptor would be present. We aimed to keep the adaptation and test different so that the measurement obtained could be attributed to the change in the after-effect and not re-adaptation to the stimulus. Again this simply highlights a difference in motivation between the research- we were interested in the variation of the after-effect following adaptation.

Measurement Period

The measurement period differs between that used by Bex at al. We sample during the recovery period (after adaptation) whilst Bex et al sample throughout adaptation and recovery. This makes sense because their motivation was to measure changes in speed sensitivity both during and after adaptation. We, however, were interested in mapping the temporal decay of the after-effect when adaptation has ceased, and therefore did not wish to sample during the adaptation period as well. Furthermore, this sampling and the presence of a test could influence the build-up of the after-effect as a critical finding about after-effects is that they are contingent on the differences between adaptation and test.

Analysis

The analysis used by Bex et al (1999) is to extract the PSE from the perceived match at each time interval, and then correlate the perceived match velocity as a measure of magnitude for each time interval. This is then fitted with an exponential function to derive a time constant for the adaptation and recovery period. This is carried out over two different speeds. The output of applying this technique is shown in Figure 5.

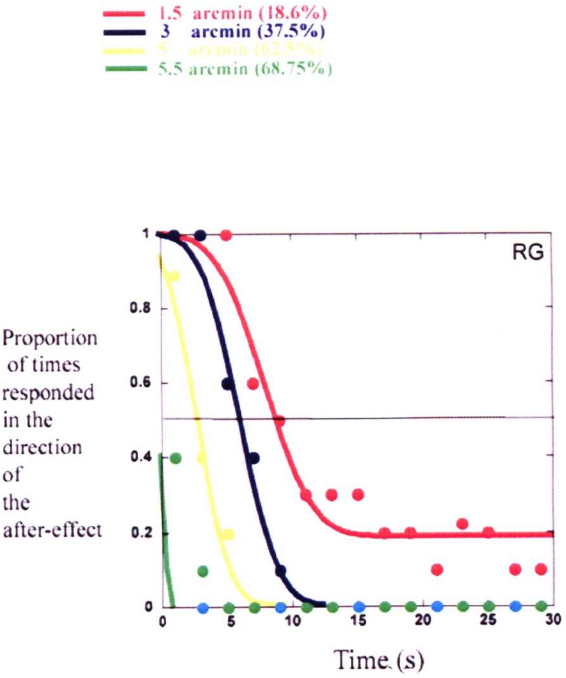


Apparent speed as a function of adaptation and recovery duration for 8-Hz (circles) and 15-Hz (squares) adapting gratings for (a) one of the authors (PB) and (b) a naive observer (RW). The *physical* contrast of standard and match gratings was equal (50%). The observer adapted to continuous motion for the first 30 s and then recovered for 30 s; apparent speed matches were measured at 3-s intervals throughout. Error bars show 95% confidence intervals. The data have been fitted by exponential functions: black curves for adaptation and gray curves for recovery. The time constants and the proportions of attenuation for each function are also shown.

Figure 5. Image taken from original paper by Bex et al (1999). Text included in order to explain results and technique.

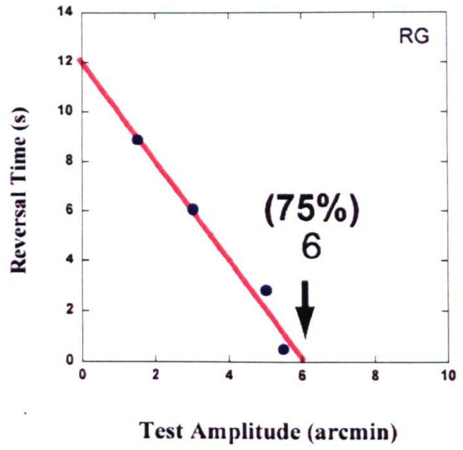
The data obtained using the matching technique described by Bex et al (1999) delivers similar, but not the same, results to the present work carried out in chapters

3 and 5 of this thesis. The results are similar in that the PSE is taken over many different levels of stimuli (varying in similarity to adaptor) using a matching technique through an adaptive procedure. In the present technique the PSE is taken from the time constant of the time to reach reversal (point where equally likely to perceive test in direction of after-effect and test). This value is completely different from the method of obtaining the time constant from obtaining the match velocity at each time interval and then correlating the match velocity with time. In the present research, the time constant obtained from the PSE's is then correlated with the strength of test presented in the recovery period, and this is used to calculate the instantaneous value of the after-effect (assuming a particular decay characteristic of the after-effect). Figure 6 illustrates the first step in the present research for obtaining an estimate of the temporal characteristics of the depth after-effect.



Figures represent the aftereffect strength for different test disparities (in arcmin and also as a percentage of adapting stimulus in parenthesis).

Figure 6. Results obtained for the depth after-effect for one observer in order to illustrate present technique. PSE is extracted from the point at which the test stimulus appears to reverse in depth over a range of test stimuli. This is a time constant and is then used to calculate the analysis in Figure 7.



Reversal times for different test disparities (RG).
Figures represent the reversal time obtained for different test disparities (in arcmin and also as a percentage of adapting stimulus in parenthesis).

Figure 7. Correlation of PSE reversal time with test disparity. This is fitted with a linear function to give a value of the after-effect at time zero.

A comparison of the results obtained in the present technique, given in Figure 7, and that obtained using the method applied by Bex et al (1999) shown in Figure 5, can now be discussed. The similarities between the techniques are that they are measuring the influence of the after-effect over different test intervals. Using both techniques gives both an estimate of magnitude of after-effect and a time constant. The most fundamental difference lies in the method used to extract the PSE and the correlation of this value with time. In the present technique proposed, the PSE is calculated from the time needed to reach a point of reversal of the stimulus (where the after-effect and test are in balance, see intersection of mid line for each test on Figure 6). This time constant is then used over a variety of tests to build up a picture of the temporal dynamics of the decay of the after-effect with time. In the technique used by Bex et al, the PSE is the match velocity obtained when adaptor and test are in balance, ***measured at each time interval.*** This value of the magnitude of the effect is then correlated with time and fitted with a function to derive a time constant of the after-effect. The impact using these two different methods is that if wishing to look at the temporal decay of the after-effect following adaptation, we wished to avoid constant re-adaptation and also keep the value constant during the testing period. This relates to the idea of the present technique as a titrating technique- the after-effect is partialled out from the signal which is the test. In the present research, the PSE is dependent on the time measure obtained with a strength of test, in the procedure used by Bex et al the PSE value is dependent on the match velocity obtained at each time interval. These techniques are therefore similar, but the subtle differences that are present may be important when interested in capturing the temporal characteristics of after-effects. Furthermore, as is highlighted by the paper discussed in the next section, the dynamics of the after-effect appear to be different between that measured during adaptation and once adaptation has ceased, with the adapted state and type of test important determinants of the characteristics of the after-effect obtained (Hammett et al, 2000). Therefore, even subtle differences in technique are potentially of maximum importance when aiming to examine the temporal characteristics of after-effect. Furthermore, we have applied this technique in the areas of motion and disparity processing. We also extrapolate to the value of the after-effect if it could be measured at time zero.

Hammett, Thompson & Bedingham (2000)

A critical paper which also seeks to address the dynamics of velocity adaptation is present is carried out by Hammett, Thompson & Bedingham (2000). Due to previous research possibly including a confound of contrast adaptation, this paper seeks to adapt to low contrast patterns and measure perceived speed at high contrast patterns. The technique employed is similar to that used by Bex et al. Specifically, an adapting pattern was presented for one of four adaptation periods. Following adaptation there was a brief interval and then the adaptation and test were simultaneously for 500msec. The test was controlled by an adaptive procedure (PEST) and was located to the right of the fixation point. The task was to indicate which patter appeared faster. When estimating recovery from adaptation pairs of adaptation and test were presented at different time intervals following adaptation (2, 4, 8, 16, 32 sec). Between each stimulus presentation a blank screen was presented. Thirty runs were taken and the 50% point estimated. The PSE was taken from 4 runs of this. This was again carried out over two speeds. The exact results of their experiment is given in Figure 8.

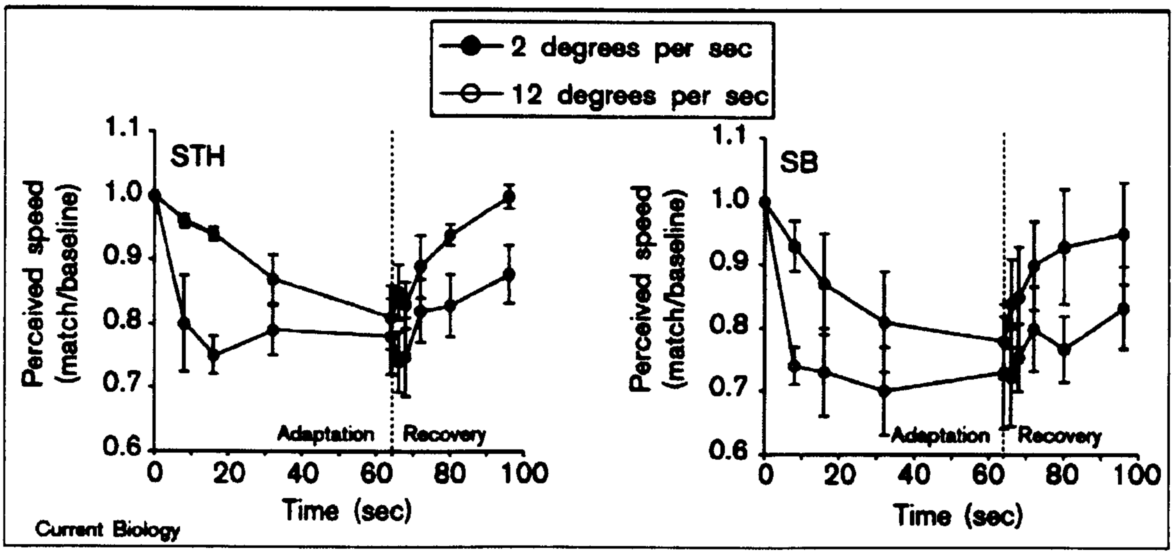


Figure 8. Results obtained using matching technique by Hammett et al (2000). Results are plotted for two test speeds and are measured during adaptation period and recovery.

The differences between this paper and the present technique are similar to those described in the previous section. The PSE is estimated from the velocity match obtained at each time interval and the PSE speed calculated for each point in time. This is then fitted with an exponential function and the time constant of the VAE taken. This is carried out for two different test speeds.

The key finding of this paper is that the time courses obtained for the after-effect recovery period do not match the exponential decay that has been found in other studies (e.g Bex et al. 1999), and used to argue for the similarity between single cell recordings from physiological research and psychophysical data. Due to this difference this led the authors to model ratio of responses at each point in time which was found to give a better account of the data.

Importantly, the authors conclude (pg 1123) that "the dynamics of the recovery phase are not simply determined by adaptation magnitude. In other words, both speed and adapted state appear to play a role in the dynamics of the recovery phase.' In the present research we measure only during the recovery period and therefore cannot be entirely sure whether to expect a clear exponential decay. In all instances, we found that in the first instance a linear approximation appeared to fit the data well and so this is how we begun.

Other differences in this paper are that the adaptor and test are present and a variety of stimuli during the test interval are also present due to the PEST matching procedure. As discussed in the previous section, this difference in methodology arises from the aim of this research in measuring the temporal variation of the after-effect when adaptation has ceased. As interaction between adaptor and test appears to be important, we wished not to have the adaptor present during the recovery period. The PSE value is calculated in a different manner in the present technique (reliant on the a time measure to reach a point of subject equality) and the time constant is then used to construct a picture of the temporal dynamics of the after-effect.

Clifford & Langley (1996)

Using part of the same protocol described previously in the work presented by Bex et al and Hammett et al, this paper seeks to model the form and time course of sensitivity changes in human motion perception and that of fly vision. They illustrate the change in perceived speed as a function of adaptation duration. They find that as adaptation duration increases, the perceived speed of the stimulus decreases.

Utilising their matching task reveals that perceived speed falls to around (75-80%) during adaptation. Their data follows the form of an exponential decay (similar to that found by Bex et al, 1999). They draw attention to the similarity of this and the decay in after-effect that has been reported by Maddess & Laughlin (1985) in measuring the H1 neuron of the fly. By modelling the data using an adaptive Reichardt detector, they provide a demonstration of the possible similarities between the human psychophysical data and that obtained from investigation of fly vision. Their results are illustrated in Figure 9.

(a) Plot of the perceived speed of an adapting grating as a function of adaptation duration for three observers. Observers were required to discriminate the speed of the adapting grating and a briefly presented test grating at a range of adaptation durations. Psychometric functions were fitted to the observers' responses independently at each duration, the points of subjective equality being used as measures of perceived speed. (b–d) Plots of the number of correct responses on a yes–no detection of a sinusoidal modulation of velocity as a function of adaptation duration. Data at two different velocity modulation depths are presented for each observer. In each case, the adapting grating had a contrast of 0.25, a spatial frequency of 0.75 cycles per degree, and a speed of 8.33 degrees per second.

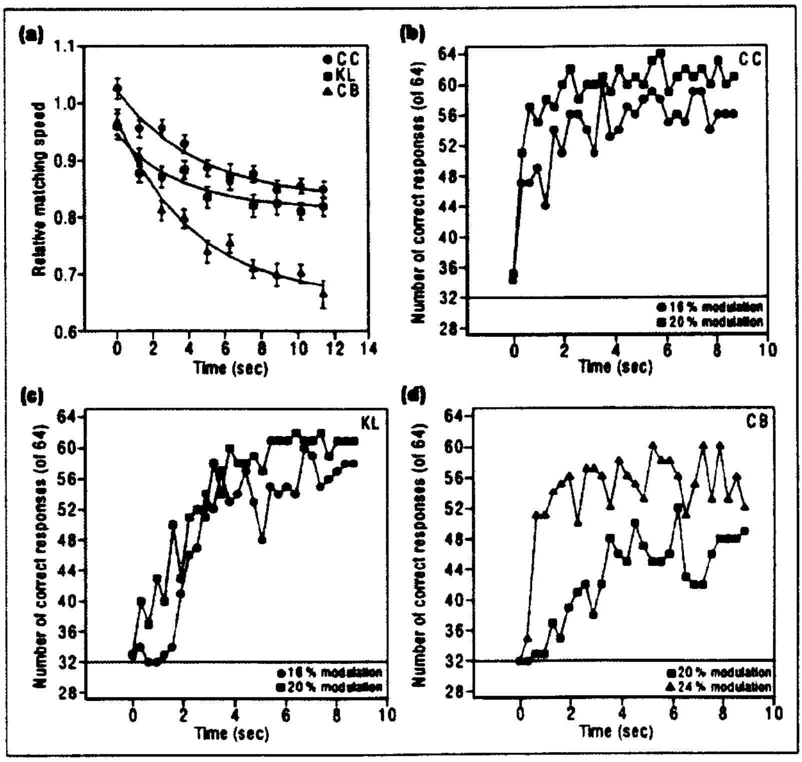


Figure 9. Results obtained in study of velocity sensitivity reported by Clifford & Langley (1996). Text taken from image. Graph (a) demonstrated the matching technique applied to obtain an estimate of the change in velocity sensitivity occurring during adaptation. An exponential decay fits this data. Graphs (b)-(d) demonstrates the detection task used to highlight the increase in sensitivity occurring during adaptation to transient changes in the adaptation velocity, (16-20% of adaptation velocity). A parallel can be drawn between this technique and the task used in the present research. The similarity is discussed in the text.

Following this measurement in reduced velocity perception, they then go on to measure the sensitivity to velocity as a function of adaptation duration. They do this through the application of a detection task in the sinusoidal modulation of velocity. They report that the number of correct detections increases as a function of duration of adaptation. As time increases from the beginning of adaptation, observers become more able to correctly identify changes in velocity.

The similarity here between their experiment and the current technique employed must be discussed. In the investigation of the depth after-effect and the motion after-effect presented here a 2 AFC detection task was used, asking is the surface in front/behind, or moving inwards/outwards? We apply this over a variety of modulations of the adaptations stimulus. This is also what Clifford & Langley (1996) report with reference to the VAE. However, we apply this to the DAE and MAE, and use the proportion correct to infer the after-effect strength as a function of time and the strength of the nulling stimulus. We also do this in the period following cessation of the adaptation rather than measuring during the adaptation period. We then extrapolate from this to obtain an estimate of the DAE strength and MAE strength at time zero for individual observers.

From the findings reported by Clifford & Langley (1996) we can conclude that in the case of velocity adaptation, there is improved sensitivity during adaptation. This is important as it may address the functional significance of the phenomena of adaptation, namely that it improves the sensitivity of a system to transient but not prolonged changes in stimulus intensity. When survival depends on being able to react to rapid changes in the environment, this information could be of extreme value.

From this work in relation to the present research we can make some predictions. That during adaptation the sensitivity to the adaptation stimulus will decrease as a function of adaptation duration. It is also possible to say that detection of small changes in the adaptation stimulus will improve as a function of adaptation duration. This was measured over a time period of approximately 12 seconds for Clifford & Langley, which is quite significantly shorter than the adaptation duration we utilised in the present research (for experimental work presented in chapter 3 & 5). This would indicate that we could expect a decay in the overall sensitivity to the adaptation stimulus (the after-effect) and that, in the case of the velocity after-effect, this could be fitted using an exponential form. Due to the increased adaptation duration used in the present experiments, we could possibly expect the decay to be greater (i.e decrease to a smaller amount of the adaptation stimulus).

Summary

If the technique employed in the studies that have been discussed in the previous section had increased the number of test speeds used, they could build up a picture of the temporal dynamics of the VAE, in a similar manner to what has been presented here. However, there would still be some crucial differences. Primarily, the estimate of magnitude of the after-effect is dependant on matching task whereas in the present technique it is a variation of a nulling technique. This is similar although not identical. Crucially, in the present work, the PSE is derived from the time taken for the after-effect to decay under varying nulling conditions. This time constant is then correlated with the strength of the test, and this is used to give an estimate of the magnitude of the after-effect. We then extrapolate from this to infer properties of the after-effect strength at time zero.

Expected decay function of the after-effect

An empirical question is how exactly to measure the explicit temporal dynamics of after-effects. It is unclear what exactly to expect. Theoretically there is a movement to avoid expressions such as 'decay' when describing an after-effect as it is viewed more as a recalibration period. The expression decay is more consistent with the fatigue model of after-effects. However, we can make some predictions based on the biological and psychophysical data that has been collected. There may also be clues from the actual neural structure of cells that would lead to a prediction of how the after-effect should decay in time.

At the neural level, in response to velocity there is a linear drop in the output from a cell recorded in the butterfly (Maddess, Dubois & Ibbotson, 1991). At first glance it may seem odd to fit an exponential to the data however there may be reasons why an exponential function appears to work. Theoretical thinking about the function of adaptation is that it may serve as a gain control mechanism. One purpose may be to increase efficiency of novel information transmission. In doing so, an exponential gain and decay would be predicted so that relative changes in the stimulus and not absolute would be propagated more efficiently. Indeed, Clifford & Langley (1996) present the similarity between the exponential decay viewed in the recovery period following motion adaptation with that recorded form the H1 neuron in the fly.

From the research just discussed related to velocity adaptation and recovery, Clifford and Langley (1996) find that the decay in perceived speed is well fitted by an exponential function to a steady level. An exponential decay function has also been used to fit the psychophysical data in velocity after-effect recovery gathered by Bex et al (1999) and by Hammett et al (2000). This accounts well for the data gathered by Bex et al, revealing time constants that compare well with physiological estimates of velocity sensitivity recovery however the same is not true of the data reported by Hammett et al (2000). A ratio model is used to describe the data reported by Hammett et al (2000).

The important question appears to be the relationship between the after-effect and the adaptation stimulus. If the relationship is proportional in terms of absolute magnitude, then it may be more reasonable to expect an exponential decay of the after-effect with time.

However, Hammett et al (2000) make clear that recovery is not determined by adaptation magnitude, speed and adapted state play a role in the dynamics of the recovery. The time course during recovery was not fitted well by an exponential function, leading them to model their responses with a ratio model. They show that even though the change in adaptation sensitivity may be an exponential decay during adaptation, the recovery phase characteristics are determined by factors such as the speed present in the test and the time used for adaptation.

In summary, it is unclear what exactly to predict as the decay function of adaptation. From the study of the response of cells, if the functional account of adaptation as an amplification of novel information is used, then it may be appropriate to use an exponential decay function. This appears to work for much of the data regarding the velocity after-effect (e.g Bex et al, 1999, as discussed in the previous section) but not all (Hammett et al, 2000). However, a further possibility is that the dynamics of after-effects may also change in regard to the after-effect in question. This may mean there is a difference in the characteristics of the recovery from depth adaptation compared to motion, however if the functional significance of adaptation is the same then a similar type of recovery pattern could be expected. One application of the current work is the beginnings of an explicit examination of the temporal dynamics of after-effects.

It should also be highlighted that similar objective techniques to the studies discussed previously in this section have been carried out (e.g Hammett, Snowden & Smith, 1993; Mollon & Polden, 1980).

The current technique would fit into a nulling test method with a bias present in the test. This method utilises duration, but by looking at the difference in duration combined with the manipulation of the bias present in the recovery period, inferences can be made about the nature of the after-effect with no test present and at time zero. This offers a clear advantage over the most popular method of measuring duration. With theory regarding the underlying mechanisms of adaptation changing to a more complex view, this technique reflects the theoretical change by offering a method of extracting the full temporal variations of after-effects. It also offers a way of overcoming the interaction of the test with the after-effect because the test is also present. The method shows exactly how the after-effect is varying with the strength of the test.

2.5.3 Motivation for development of technique and current findings

It has been suggested that one reason for the lack of a clear theoretical framework is the use of inconsistent techniques and poor methodology (Pantle, 1998) and the present research attempts to address this issue through the development of a psychophysical technique that could accurately measure after-effects in the visual system. This technique is a novel contribution in 3 ways: (1) it allows the inference of the strength and magnitude of the after-effect at time zero, (2) it allows a picture of the temporal dynamics of the after-effect in terms of strength and time duration and (3) it gives a method of assessing the interaction of test and the after-effect throughout the duration of the effect. This allows for a more accurate measurement of adaptation and after-effect. This provides an excellent starting point for future models investigating the underlying mechanisms of adaptation in the visual system.

From the results obtained in the research presented here it is also clear that there are different mechanisms underlying motion and depth processing in the visual system. In order to capture this difference it is necessary to develop an underlying framework for understanding adaptation. The contribution of this work is a method which allows a strong platform to do so, as we have developed an accurate way of measuring after-effects following adaptation in any visual domain.

In three of the experiments presented in this thesis we specifically investigated the temporal dynamics of after-effects. We aimed to apply a novel method in which to do this. By using a test stimulus that was identical to the adaptation, and varying the amount of bias in the test stimulus, we created a situation in which there was a reversal of the after-effect. By manipulating the amount of bias in the test stimulus, this changed the length of time the after-effect appeared to dominate the test. By looking at the relationship between the period of time taken for the after-effect to diminish, and the nulling required in the test stimulus, the full temporal variation of the after-effect could be captured. This provided a way of mapping both the magnitude and its variation with time for each test. Additionally, it provided a way of working out the instantaneous strength of the after-effect, and duration, critically when no test is present. As this is an important issue in research regarding after-effects, and the theoretical move towards more complex sites of processing and the findings regarding adaptation and test structure, this technique is a useful addition to the methods already employed.

Indeed, the current technique employed can be seen as a development of other nulling techniques. The difference is that the percept is tracked over time, whilst being nulled by a number of parameters, giving an indication of the relationship of the magnitude and strength of the after-effect as it changes over time. By obtaining the Point of Subjective Equality (PSE) for this relationship, the strength and duration of the after-effect for each individual observer can be mapped out and the initial strength and duration measured.

Chapter 3: Temporal Dynamics of the Depth After Effect.

3.1 Overview

Following prolonged exposure across a particular stimulus domain (known as adaptation), a change in perception occurs which can be referred to as an after-effect. This change in perception can be used as a psychophysical demonstration for mechanisms selectively adaptive to properties of the visual image. This has led to the adaptation paradigm becoming increasingly popular as a tool for investigating the underlying mechanisms of visual perception. However, as after-effects are a delicate and subjective phenomenon, the techniques used to measure the degree and time course of the adaptation have faced difficulty. The two main challenges have been: (i) minimising the influence of the precise nature of the testing stimulus on the measurement of the after-effect and (ii) the variation of the magnitude of the after-effect with time. In this experiment we develop a technique for measuring an after-effect and capturing its full temporal variation. We first apply this technique to the Depth After-Effect.

3.2 Introduction

Despite recent theoretical changes regarding the functional role of adaptation as critical in a dynamic recalibrating visual system (Wade & Verstraten, 2005), current models of stereopsis do not take account of adaptation (Mayhew & Longuet-Higgens (1982); Erkelens, van Ee (1998)). Investigating the exact nature of the temporal dynamics of the adaptation process involved could offer insight into the investigation of underlying mechanisms of depth perception.

The Depth After-Effect can be observed following prolonged exposure to a surface located at a certain depth. Following adaptation, the perception of a subsequent test surface is non-veridical: it is perceived as either in front or behind the adaptation surface (the reverse of the adaptation stimulus), (Blakemore & Julesz, 1971). This means that if exposed to a surface that is close to the observer for a period of time, a similar surface presented at the same location will subsequently be perceived as further away.

The output of the present research has been the development of a novel technique that provides a method for the capture of the full temporal dynamic of this effect. This includes an estimate of how the after-effect strength is varying with time following adaptation. Furthermore, this method offers an estimate of the strength and time course of the after-effect at time zero.

This chapter begins with an outline of the method by which we arrived at the best stimuli for obtaining strong after-effects. It was clear from this work that the strength of the after-effect varied with the type of stimuli used and also the length of the adaptation time. The chapter first begins by outlining the previous work looking at the depth after effect and its variation in time.

3.3 Previous Work

Depth mechanisms have previously been identified using adaptation (Blakemore & Julesz, 1971; Long & Over, 1973). It is apparent that after-effects occur in many modalities – colour, motion, and orientation- but of interest here is the depth after-effect. The basic paradigm utilised in the measurement of this after-effect is best described by looking at the first published experiment in this area. The experimental research in this area relies on variations of the techniques carried out by Blakemore & Julesz in (1971). In this experiment a pair of vertically separated disparate squares with disparities of +2 and –2 arcmin of disparity (with respect to the fixation bar) were depicted using a random dot stereogram (RDS). An RDS is a stimulus created by randomly allocating dots in an 2Dimage and then moving the position of these dots in relation to the two eyes. When viewed stereoscopically, this produces a 3D image. Random dot stereograms are ideal for use in such an experiment as there is no monocular information relating to depth and therefore any perception of depth must arise from the information derived from binocular disparity information.

The technique employed is to fixate (adapt) to the surface specified by the disparity defined in the RDS and then transfer gaze onto a similar stimulus and measure the subsequent perception of depth. Following the adaptation period, the perception of the subsequently viewed stimulus (the test) is altered such that the depth is in the opposite direction to adaptation stimulus (see Figure 2 for an example of this). By verbally estimating the duration of the after-effect and then introducing disparity into the test to see how much disparity was needed to make the after-effect disappear, the strength of the after-effect was inferred. In their experiment they reported that following adaptation to +2 and –2 arcmin of disparity for 2 minutes, a +ve disparity being a point which lies in front of fixation whilst a –ve disparity lies behind the point of fixation. Following this period of adaptation, it was reported that the after-effect persisted for a period of up to 5 minutes with 30 arcsec of disparity required to null the after-effect (Blakemore & Julesz, 1971).

The important contribution of this research to the knowledge of the depth after-effect was that firstly an alteration of depth perception could be induced due to prior exposure to a disparate stimulus. This result demonstrated clearly that binocular disparity is an important cue to depth. Secondly, (accessed through verbal reports) a relationship between the amount of disparity in the test stimulus and the duration of the after-effect was established. This was done by verbally reporting the duration of the illusory depth induced by adaptation. By increasing the adaptation exposure duration the duration of the after-effect was increased. These are important contributions because they mark the starting point of the investigation of the interaction between depth perception, adaptation time and disparity. Also, the fundamental concepts of the inference of strength of after-effects through the 'nulling' technique and estimation of duration of the after-effect were introduced. These findings have since been supported (Long & Over, 1973; Mitchell & Baker, 1973; Graham & Rogers, 1982a; Rose & Price, 1995) again demonstrating that binocular disparity is a consistent cue used in the recovery of depth. Upon further investigation of the after-effect it is clear that there is a relationship between the period of adaptation and the persistence of the effect (Long & Over, 1973) and also that the magnitude of the effect is related to not only the disparity present in the adaptation stimulus but the disparity of the adaptation relative to the test stimulus (Lee, 1999). In general it appears that the initial after-effect occurs only for the first few seconds and only over a certain range of disparities (Howard & Rogers, 2002). The largest effects have been reported over relatively small disparities of 2 arcmin (Blakemore & Julesz, 1971), 4 – 8 arcmin (Long & Over, 1973) and 2.5 arcmin (Graham & Rogers, 1982a) with up to 85% of the strength of the adaptation stimulus being introduced to null out the after-effect (Graham & Rogers, 1982a). The effect is dependent on the time used for adaptation and the amount of disparity in both the test stimulus and the adaptation stimulus. The after-effect disappears at larger disparities (~20 arcmin – Howard & Rogers, 2002). It is unclear exactly why the effect disappears at larger disparities. The variation has predominantly been in the type of stimuli used – with the major difference being whether the stereogram depicted squares in depth or a corrugated surface. Although all these studies can give an indication of the strength of the after-effect and roughly how long it lasted, given the rapid dissipation of the after-effect and its interaction with the test stimulus, the strength and change of the after-effect with time has not been fully quantified.

3.4 Aim of present research

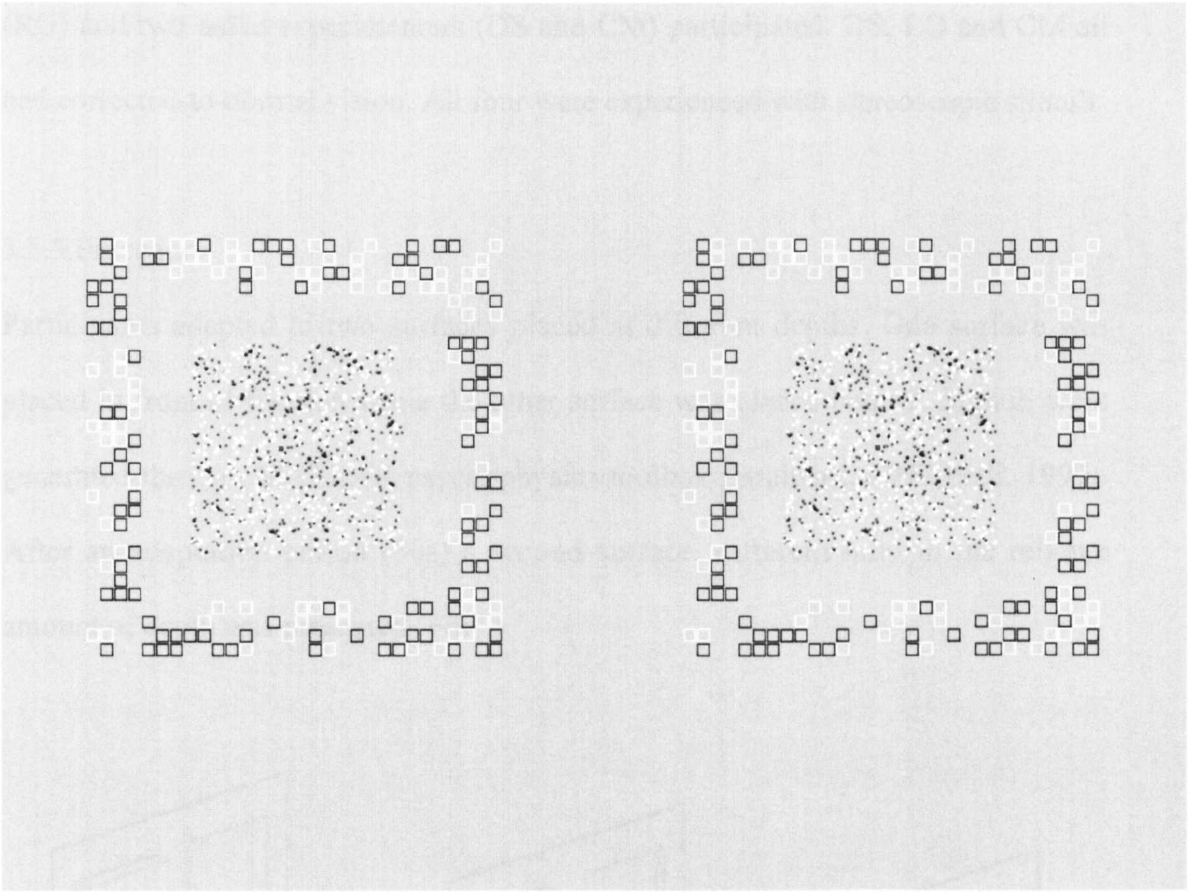
The first step in the present research was to develop a method of capturing the full temporal dynamics of the after-effect. Many of the previous experiments had inferred depth from the amount of disparity required to null the after-effect, (Blakemore & Julesz, 1971) and typically relied on subjective estimations of duration such as verbal reports (Mather, 1998).

3.5 Methods

3.5.1 Stimuli

A number of different stimuli were investigated before a suitable test stimulus was decided upon. The stimulus yielding the most persistent after-effect was selected. An example pilot stimulus is illustrated in Fig. 1.

The stimuli used in the final experiment were two surfaces, which were depicted by horizontal disparity, similar to the Blakemore & Julesz (1971) setup described earlier.



Left Eye Image Right Eye Image

Fig 1: Example used to illustrate stimuli investigated for initial experiments researching the depth after effect. Image depicts a corrugated surface using binocular disparities, with surrounding frame used to assist maintenance of vergence. Similar to this, a flat surface was also tested using both a moving and non- moving probe.

3.5.2 Observers

There were four participants in this experiment. The author, one non-naïve observer (RG) and two naïve experimenters (DS and CM) participated. DS, LO and CM all had corrected-to-normal vision. All four were experienced with stereoscopic stimuli.

3.5.3 Procedure

Participants adapted to two surfaces placed at different depths. One surface was placed in front of fixation while the other surface was placed behind. Stimuli were generated through MATLAB psychophysics toolbox (Brainard, 1997;Pelli, 1997). After an adaptation period (30s) a second surface, different only in the relative amount of depth was presented (Fig 2).

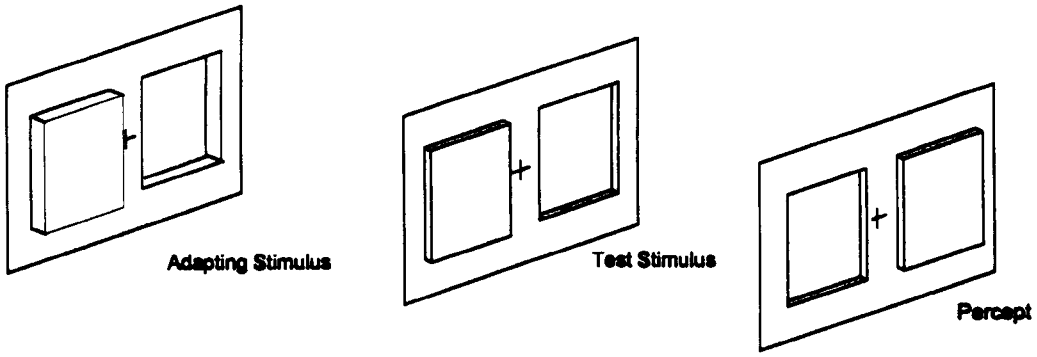
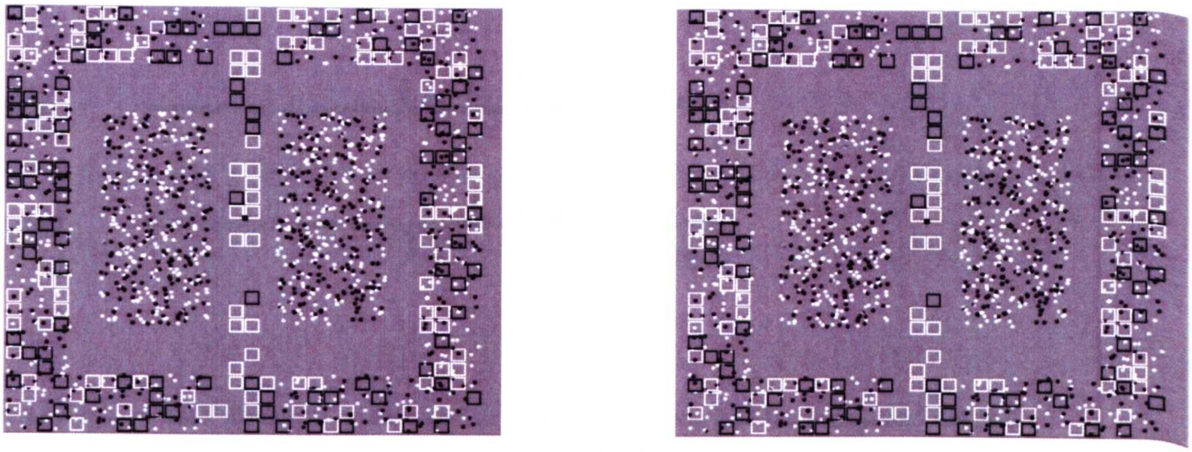


Fig 2: Stimulus used for experiment.

In Figure 2 the adapting stimulus is shown on the left and the test stimulus in the centre. Following adaptation the test stimulus appears to have the pattern of depth shown on the right of Figure 2. Due to the after-effect, the test stimulus is initially perceived with a reversed depth and gradually returns to its veridical depth. Therefore, it was decided to track perceived depth by asking the observer to make regular judgments during the testing period. It is predicted that perception will change in a direction consistent with the perception of an after-effect. Specifically, it is predicted that the after-effect will dominate perception initially and this will recede as time progresses. The time constant that it takes for this after-effect to recede is a measure of the duration of the after-effect.

We used a two alternative forced choice task setup and the method of constant stimuli. Three observers adapted to a stimulus with 8 arcmin of disparity while one observer (DS) adapted to a stimulus with 30 arcmin disparity. Adapt duration was 30 seconds. Four observers (two naive (CM, DS), two non naive (RG, LO)) carried out 10 repeated trials at a minimum of 4 test disparities. All were then presented with test disparities at varying percentages of the adaptation disparity, varying from ~20% to 90% of the adaptation disparity (see Fig 3 for exact figures). The surfaces were defined by the disparities of random dots refreshed every half second. We aimed to control vergence by using a surrounding texture placed at zero disparity (see Fig 5). The entire stimulus image was 9x9 degrees of visual angle. It consisted of two surfaces next to each other surrounded by a frame. Each surface measured 2.25 degrees horizontally by 4.5 degrees vertically. The surface defined by disparity was created as follows: 500 black and white dots (50/50%) were generated at random locations and placed on the stimulus surface. The dot density was thus 49 dots degree^{-2}. The disparity was created using orthographic projection. The dot size was 4 min of arc radius.



Left Eye Right Eye

Fig 3: A two surface stereogram was generated which depicted a depth separation between surfaces, with one side closer to the observer than the other.

During the first 30 seconds of a trial the observer made no response. This was the adaptation phase of the experiment. Following a brief interval, a surface similar to the adaptation stimulus was presented for 30 seconds at a disparity that was chosen differently from trial to trial. During this test phase, participants were asked to judge the perceived depth (in front or behind) of one surface relative to the other at the sound of a beep presented on average every 2 seconds. Fig 4 is an illustration of the time course of the experiment.

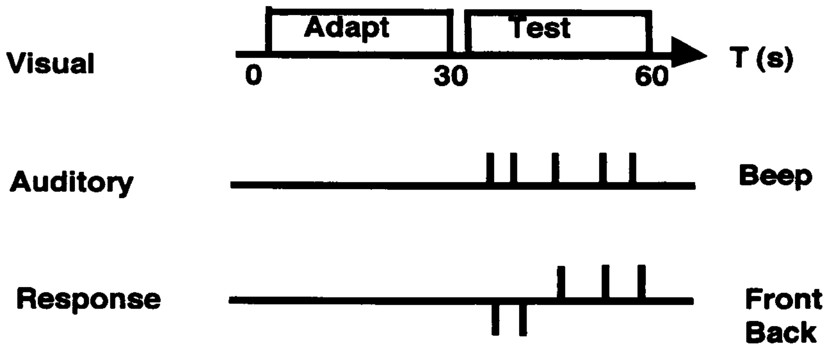


Fig 4: Time course of trial. Observers were asked to fixate on the centre of the screen and did not respond for the first 30 seconds of the experiment. This was the adaptation phase. Following a brief period, a test surface appeared and observers were asked to judge the perceived depth of the surface on average every 2 seconds. These data were then used to build a psychometric curve reflecting the perception of depth at each disparity tested. We did this in order to build up a data set reflecting the relationship between disparity and the strength of the after-effect following a period of adaptation.

3.5.4 Apparatus

The stimuli were generated on an Apple G4 and presented using a Wheatstone stereoscope setup placed on a SONY Trinitron 21" monitor using a refresh rate of 75hz and a viewing distance of 800mm, set at a resolution of 1152 x 870 pixels. A chin and forehead rest was used in order to maintain fixation.

3.6 Analysis

This experiment has two independent variables: the amount of disparity in the test stimulus (4 levels) and the time at which the test stimulus occurs following the adaptation period (15 levels). One dependent variable was measured for each time and test disparity. This was a judgement of the perceived depth of the test stimulus. In order to obtain these data the proportion of responses in the direction of the after-effect was recorded as a function of test disparity and time. The strength of the after-effect represents the proportion of times the test stimulus was perceived with a depth predicted by the after-effect. The effect was strongest for small disparities and decreased as the amplitude of the test surface increased. A "reversal time" of the after-effect was defined as the time needed to reach the point of subjective equality (the point at which one surface was seen equally often in front or behind the other surface). These reversal times were obtained after fitting the data with the compliment of cumulative Gaussian (i.e 1-cumulative Gaussian), and were estimated for each observer at each level of test disparity. The data were fit using the method of least squares. The reversal times were then plotted with the test disparity and a linear regression is applied to find an estimate of the after-effect at time zero.

3.7 Results

The strength of the after-effect here is taken as: ***the proportion of times the test stimulus is perceived in the direction of the after-effect.*** Using this as our definition of after-effect strength then Fig. 5 (a,b,c &d) shows how this proportion varies with time, which is referred to as after-effect strength. As can be seen from the graphs, the temporal dynamics of the after-effects are varying with the disparity of the test surface. At different levels of disparity the after effect strength and duration is changing, as represented by the different curves on the graphs. For increasing disparity introduced into the test stimulus the after-effect decreases in strength and time. Fig 6 shows that reversal times are linearly related to the test amplitudes. The intersection of this line with the abscissa provides an estimate of the disparity that would instantaneously null the after-effect.

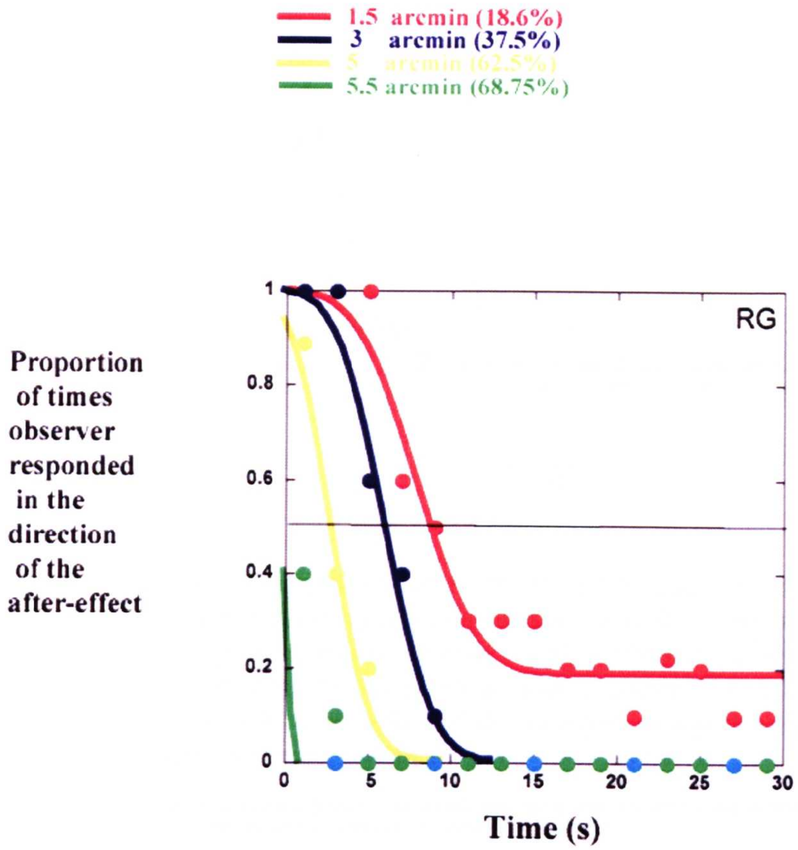


Fig 5a. Temporal Variation of the Depth After-Effect (RG). Figures represent the proportion of times the observer responded in the direction of the after-effect at each time interval. Figures represent the effect obtained for different test disparities (in arcmin and also as a percentage of adapting stimulus in parenthesis).

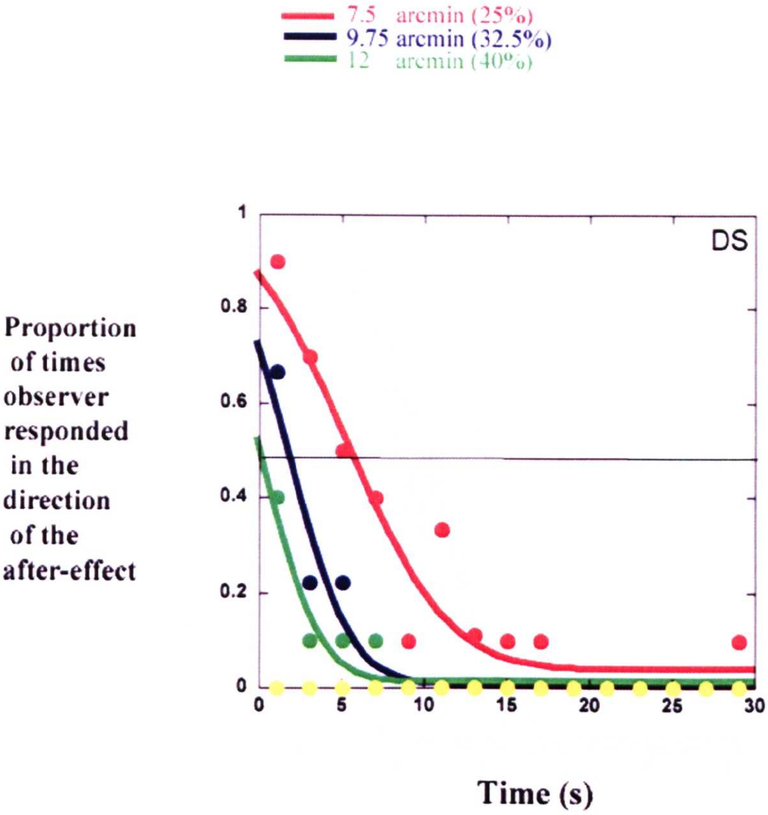


Fig 5b. Temporal Variation of the Depth After-Effect (DS). Figures represent the proportion of times the observer responded in the direction of the after-effect at each time interval. Figures represent the effect obtained for different test disparities (in arcmin and also as a percentage of adapting stimulus in parenthesis).

***Yellow points indicate disparity where DAE was nulled instantly for observer and no reversal time obtained. This occurred for a disparity of 14.25 arcmin (47.5%)**

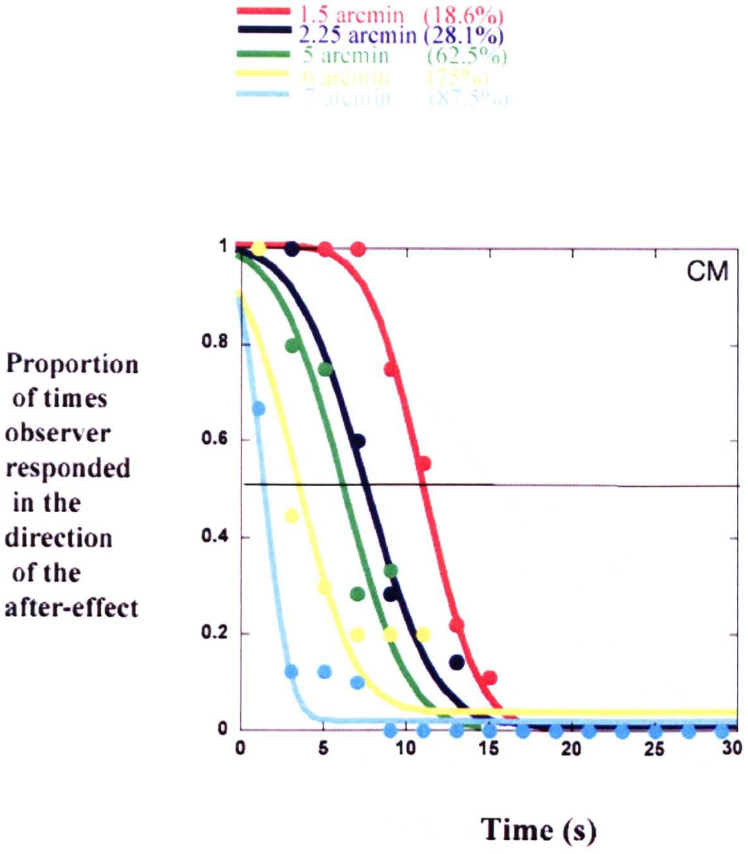


Fig 5:c. Temporal Variation of the Depth After-Effect (CM). Figures represent the proportion of times the observer responded in the direction of the after-effect at each time interval. Figures represent the effect obtained for different test disparities (in arcmin and also as a percentage of adapting stimulus in parenthesis).

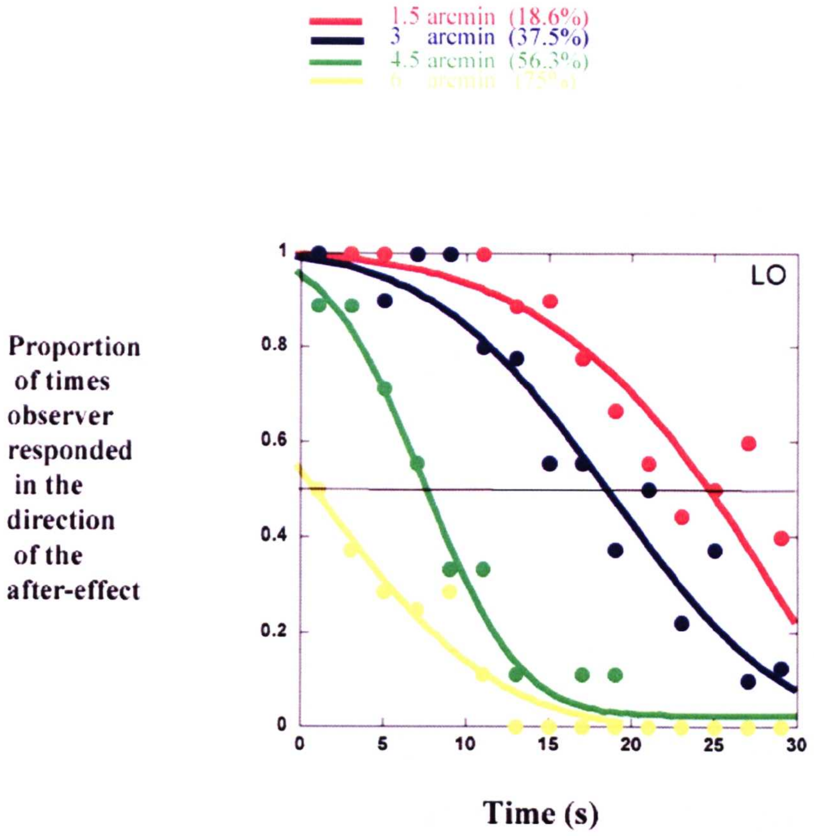


Fig 5d. Temporal Variation of the Depth After-Effect (LO). Figures represent the proportion of times the observer responded in the direction of the after-effect at each time interval. Figures represent the effect obtained for different test disparities (in arcmin and also as a percentage of adapting stimulus in parenthesis).

From the individual data collected and shown in Fig 5 for each observer (a,b,c & d), the PSE for each of these curves was calculated. This is what we refer to as a reversal time. Fig 6 (a,b,c & d) shows these reversal times obtained for different test disparities. Each graph indicates the reversal point obtained for each observer. Participants were tested with a minimum of 4 tests (RG, LO, DS) and a maximum of 5 (CM). It should be noted that for participant DS, two out of four of the values fell on 0 and .1 which gives the impression of only two points on the graph, though four data points are present.

An exponential function was also fitted to the PSE data obtained for each observer. The linear and exponential functions, in terms of the coefficient of determination, R^2 was determined. The value obtained for each observer for both types of fit are listed in Table 1.

Observer	Linear Fit (R^2)	Exponential Fit (R^2)
RG	.97701	.87242
DS	.95255	.96206
CM	.91183	.87637
LO	.9886	.80567

Table1. Comparison of linear and exponential functions fitted to the PSE data obtained for each observer.

A linear regression appeared to fit the data well and was therefore used in the subsequent analysis. Different observers carried out different contrasts as these were the values at which a reversal of depth was obtained. The individual difference found in the overall sensitivity to the depth after-effect in this experiment is presented in the discussion.

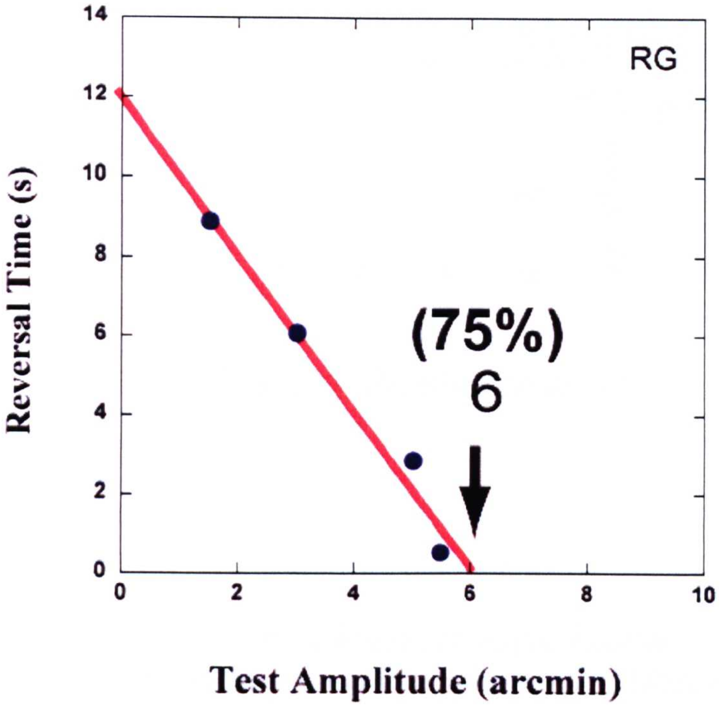


Fig 6a Reversal times for different test disparities (RG).
Figures represent the reversal time obtained for different test disparities (in arcmin and also as a percentage of adapting stimulus in parenthesis).

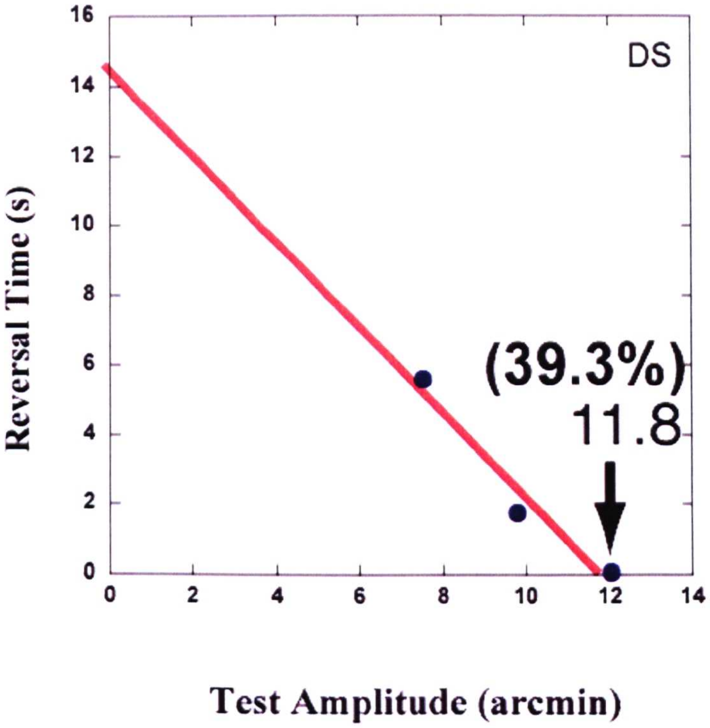


Fig 6b Reversal times for different test disparities (DS).
Figures represent the reversal time obtained for different test disparities (in arcmin and also as a percentage of adapting stimulus in parenthesis).

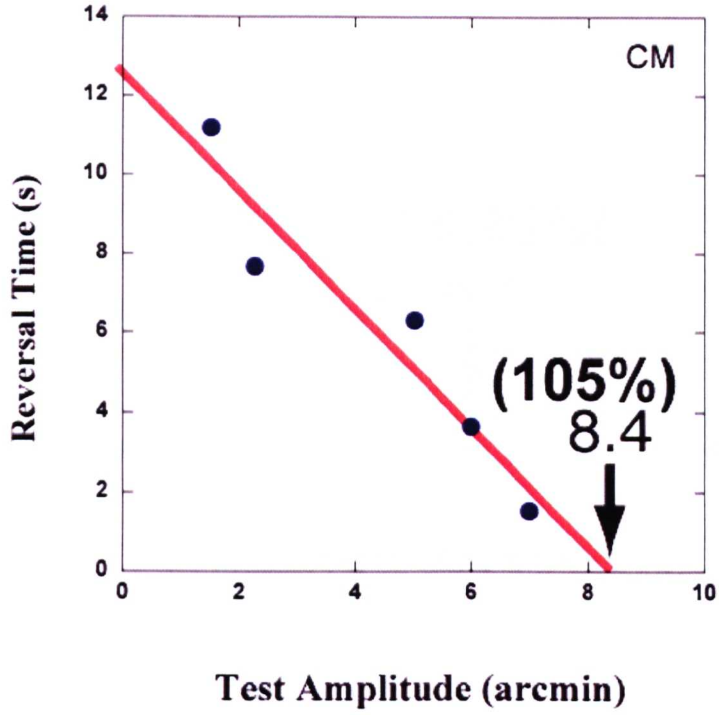


Fig 6c Reversal times for different test disparities (CM).
Figures represent the reversal time obtained for different test disparities (in arcmin and also as a percentage of adapting stimulus in parenthesis).

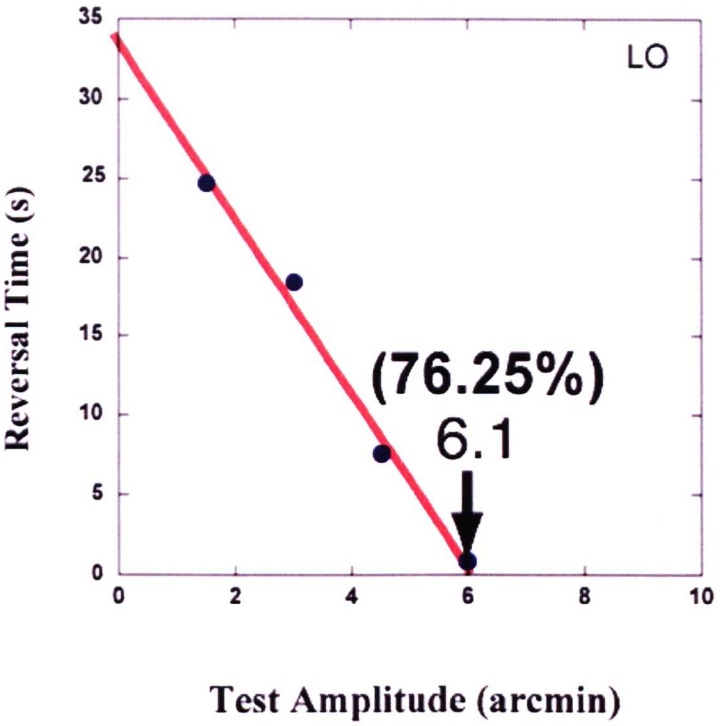


Fig 6d Reversal times for different test disparities (LO).
Figures represent the reversal time obtained for different test disparities (in arcmin and also as a percentage of adapting stimulus in parenthesis).

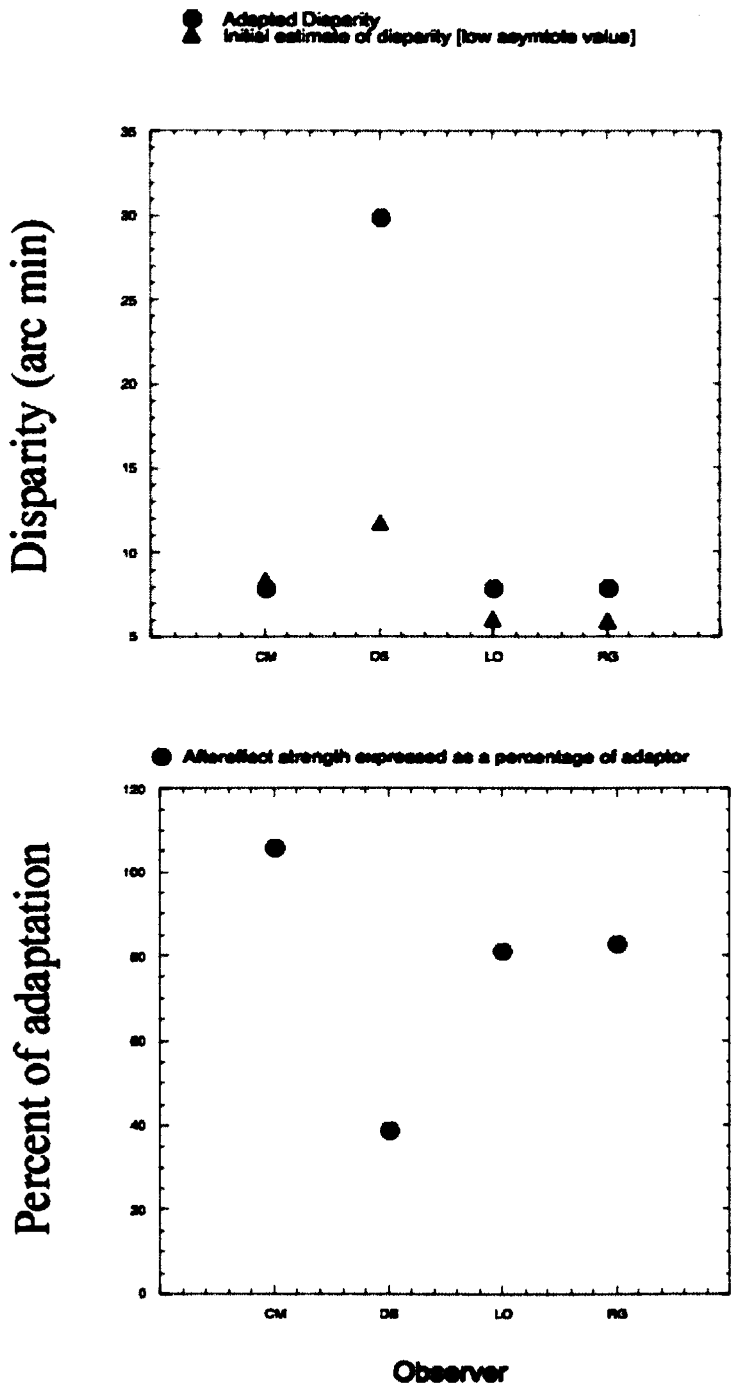


Fig 7: (a) *top graph illustrates the estimate of the disparity at time zero and (b) (lower graph) illustrates the after-effect strength expressed as a percentage of adaptor.*

3.8 Discussion

Previous work has demonstrated that a depth after-effect could be obtained following exposure to random dot stereograms (Blakemore & Julesz, 1971; Long & Over, 1973; Graham & Rogers, 1982a; Rose & Price, 1995). This work has also revealed that the depth after-effect is spatially localised and tuned for disparity (Kohler & Emery, 1947; Mitchell & Baker, 1973). In these previous studies a nulling technique was commonly employed to estimate the magnitude of the after-effect. Duration has also been a method of measurement though not as popular as nulling techniques. In this experiment we apply a nulling technique, however we track the observers' percept during the testing period. We present the results of measuring the temporal variation of the depth after-effect in terms of strength and duration. These results were obtained for four observers and the implications of these results are now discussed.

3.8.1 Temporal variation in strength

Our index of strength was the proportion of responses made in the direction predicted by the after-effect (opposite to the disparity presented during the adaptation phase). These results indicate that the after-effect peaks at the beginning of the testing period and then decreases as the testing period progresses. This result holds for every disparity tested. As the amount of disparity in the test increases, the strength of the after-effect decreases. This pattern holds for every observer tested.

3.8.2 Strength at time zero

Using this technique it is possible to make an inference of the after-effect strength at time zero. From analysing the time to reach the PSE using different tests of varying disparity it is possible to look at duration as a function of test disparity. In this experiment, the relationship between the test disparity and the strength of the after-effect appears to be linear (see Fig. 6). By carrying out a linear regression analysis on the data obtained, it was possible to estimate the disparity value that would be required to instantaneously null the after-effect. This was carried out for each observer. Fig 7 is given to illustrate the estimate obtained for the disparity at time zero using the fit obtained in Fig 6. This is expressed in absolute values and as percentage of adaptor (Fig 7 a,b respectively).

The results for the instantaneous value of the after-effect showed considerable inter-observer variation. The strength of the after-effect is very strong for some observers (106% in one case, observer CM) and weaker for others. Graham & Rogers, 1982a report an after-effect of up to 85% whilst other studies have revealed after-effects of up to about 25%.

Predictors of depth after-effect strength include disparity gradient with the usage of continuously varying disparity profiles yielding a larger effect than discrete depth planes (Howard & Rogers, 2002). Pilot work in this experiment suggested that this was not the case as the after-effect observed was brief in these conditions. Another factor is the topping up procedure utilised in other experiments (Graham & Rogers, 1982a). As topping up methods have proved important in determining the strength of the after-effect, it is possible that re-adaptation could have occurred in these experiments, similar to 'topping up' between adaptation sessions. The sessions were blocked, however it is possible that some of the adaptation could have built up between sessions. However, the relationship between increasing test disparity and decay of the after-effect was maintained despite variation in the order of test presented, indicating that the influence of this was minimal.

A possibility for the results obtained in the literature and also the wide variation of results obtained here is intersubject variability in the perception of depth. It has been suggested that approximately 30% of the population exhibit some form of stereoanomaly (Van Ee & Richards, 2002). This supports the idea that individuals differ markedly in how much depth is seen for a given stimulus disparity. A high gain relationship between depth and disparity has been seen indicating that for some observers even a small disparity can elicit a large depth magnitude. Similarly, in some cases over an entire range of disparities very little depth is seen. Asymmetries have also been demonstrated in the gain relation between depth and disparity for crossed and uncrossed regions over individuals. There are variations in the detection of very fine or large disparities and also for points near and far away from the observer (Braddick, 1982)

If individual difference in disparity and depth perception underlie the results obtained, this technique could be applied in the investigation of such phenomena. As the after-effect is necessarily a subjective phenomenon this offers another method of capturing the effect and individual variations in response to adaptation.

3.8.3 Duration

Persistence

The duration of the depth after-effect has been related to the adaptation time, and reported verbally to increase up to a limit of 5 minutes (Blakemore & Julesz (1971). In this experiment the duration of the after-effect was taken as the time to reach the PSE in the testing phase. This time constant decreased with increasing disparity used in the test stimulus. For three of the observers tested, all durations recorded of the after-effect were less than 12 seconds. Observer LO however demonstrated a longer after-effect, which persisted for almost 25 seconds when the smallest test disparity was used.

Measuring the after-effect by this method also offers an objective method of estimating the end of the after-effect. In previous studies either a test stimulus was nulled until it appeared flat, or the disappearance of the effect marked by verbal report. This method gives an estimate of the end of the perception of the after-effect.

3.9 Conclusion

In this experiment we sought to measure the temporal dynamics of the depth after-effect. In doing so, we tracked the change in perception of the observer over time, giving an estimate of how the strength is changing over time. This method offers a way of estimating the instantaneous value of the after-effect and also gives a way of estimating the end of the effect[3]. In this experiment the relationship between depth and disparity was found to be linear, however there was considerable intersubject variation in the values obtained. It can also be argued that an exponential function could be used to fit the PSE value. A comparison of these values is carried out in Table 1. In nearly every case the linear value appeared to give a better fit to the data and therefore we used this as our approximation of the decay function.

One finding in depth research is that there are large differences between observers in the perception of depth from disparity, which could be highlighted by using this technique. The method gives a method of accessing for individual observers the precise strength and duration of the after-effect.

There is less variation between observers in perception of motion. The next step in the research presented here was to examine the temporal dynamics of the motion after-effect.

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[3] This is true only if the decay function of the after-effect is known. In this experiment, we found that a linear approximation of the results appeared to fit the data (see Table 2) and therefore we proceeded with a linear fit to make this inference. In other types of after-effect it may be more appropriate to use an exponential fit to the data.

Chapter 4: Temporal Dynamics of the Motion After-Effect

4.1 Overview

After-effects occur in many modalities including colour, orientation motion and depth. Following development of a technique for measurement of the magnitude and duration of an after-effect (and the application of this to the depth after-effect outlined in the previous chapter), this experiment investigated its application in the area of motion perception. Here we aimed to capture the temporal variation of the motion after-effect (MAE).

4.2 Introduction

In evolutionary terms, the goal of perceptual processing is to enable survival amidst an environment that is constantly changing. This is critical because without knowledge of the position of objects (or itself) in the environment, an organism will fail to achieve necessary biological aims, such as hunting for prey or conversely, surviving attacks from predators. Consequently, underlying mechanisms of visual processing have the task of arriving at an estimate of motion in the environment and any theory of visual processing must include how this relates to the overall processing of visual information.

In order to arrive at accurate knowledge of motion in the environment an organism requires at least two sources of information: knowledge of (i) the speed the object is moving at and (ii) the direction it is moving in. Current theories of visual processing focus on the encoding of this information through populations of neurons sensitive to speed and direction of motion, however, quantifying the underlying mechanisms of motion processing remains a hotly debated area of research.

One aspect of motion processing that has been investigated intensively is the change in perception that occurs following prolonged exposure to visual motion. The most common manifestation of this perceptual change is the experience of illusory motion moving in a direction opposite to the motion that was adapted to. This is sometimes referred to as "The Waterfall Illusion" because it can be experienced by staring at a waterfall for approximately 30 seconds and then transferring the gaze to the adjacent rocks, which then appear to be moving upwards (i.e. opposite to the direction of motion first experienced, the downwards falling water). This perceptual after-effect, termed the Motion After-Effect (MAE), has been utilized in a variety of ways for researching the underlying mechanisms of visual motion processing (Anstis et al, 1998).

This approach has been fruitful. For instance, study of the MAE has generated theoretical propositions concerning the underlying differences between first- and second-order motion (Nishida & Sato, 1995). It has also contributed to knowledge of the differential processing of fast and slow moving information present in the environment (Verstraten, 1998). However, as the MAE is a delicate and subjective phenomenon, much of the research has been challenged by the development of adequate techniques and consistent methodology (Pantle, 1998).

Indeed, many techniques have been applied in the investigation of the MAE. Initially, the basic paradigm was to have observers adapt to a uni-directional moving stimulus and then present a static stimulus of the same dimensions (Sekuler & Pantle, 1967). Observers would then perceive movement in the opposite direction to that in the adaptation stimulus. In order to quantify the magnitude and duration of this effect, subjective measures were recorded such as verbal reports of the speed and adjustment of a dial to indicate the change in strength over time (Howard & Rogers, 2002). These measures were helpful in establishing that adaptation strength and duration altered during what was termed a 'recovery' period. All these tests contributed estimates of the properties of the MAE, which were reliant upon presenting a stimulus that was a static version of the original moving adaptation stimulus (see Pantle, 1998 for a review).

Such methods yield an estimate of the after-effect for a static test; however, there is currently evidence to suggest the existence of two different types of after-effect, elicited by different test structures and possibly representing the existence of different motion processing mechanisms in the brain. Therefore, using such a technique will only deliver information on the nature of a static after-effect. This is problematic in theory, too, as the motion after-effect is difficult to quantify because it is often experienced as illusory motion that is known to be static at the same time (Anstis et al, 1998).

The research has progressed with the introduction of dynamic test gratings and the corresponding measurement of the after-effect. A dynamic test grating is usually a flickering test stimulus, where the direction is ambiguous rather than static (Levinson & Sekuler, 1975). For example, by placing two super-imposed sine wave gratings, two motion after-effects can be induced (Pantle, 1978). This creates a transparent stimulus made by the two adapting components moving in opposite directions. By keeping one of the sine waves constant and varying the temporal frequency of the second sine wave, the two after-effects can interact so as to create a static sine wave. The characteristics of the second varied sine wave can be used to study the properties of the motion after-effect. For example, the contrast and the temporal frequencies can be changed in order to null out the MAE. This technique has since been used with isotropic random dot patterns (Mather, 1980) and random pixel arrays (Verstraten et al, 1994a). Interestingly, it was found that the MAE varied as a function of the speed of the second component of the adaptation stimulus and that for different as well as equal speeds of the adapting components the direction of the combined MAE could be predicted from the vector sum of the adapting components provided that their magnitudes were made proportional to the MAEs they produced individually.

The main conclusions to be drawn from the previous research are that there appear to be at least two MAEs which can be elicited using static or dynamic gratings (although some dispute this e.g Nishida et al, 1997a). This has led to the proposal of multiple encoding sites of motion in the brain and the hypothesis that there are at least two distinctive temporally tuned channels involved in the processing of motion (Verstraten et al, 1995). The differential effects of storage, attention and interocular transfer on the static versus dynamic testing of the MAE does support such a distinction (Culham & Cavanagh, 1994; Lankheet, 1995; Anstis, 1998) however these results are not always consistent across studies (McCarthy, 1993; Nishida, 1997a; Pantle, 1998).

The aim of this experiment was to obtain access to the temporal dynamics of the MAE. We initially proposed an experiment using both a static and moving test. We sought to measure the perception of the after-effect as it changed over time for each observer. The specifics of the experiment are described in the following section.

4.3 Methods

4.3.1 Method

In this study, participants were adapted to motion in a given direction (right or left) for a period of 20 seconds. They were then presented with a similar test field which differed in the velocity it was presented at and was presented at a slightly reduced contrast. Over repeated presentations of a test stimulus, observers made a judgment on the ***direction*** of motion. From previous research on the decay of the after-effect it was predicted that the after-effect caused by the motion adaptation would be initially strong and gradually decay as a function of time. In this experiment, due to adaptation, we predict that observers initially see motion in the direction of the after-effect and this would gradually change to motion in the true direction (all motion in the direction of the after-effect must be illusory as the test stimulus is always in the direction of the adaptation stimulus). The idea here is illustrated in Fig 1.

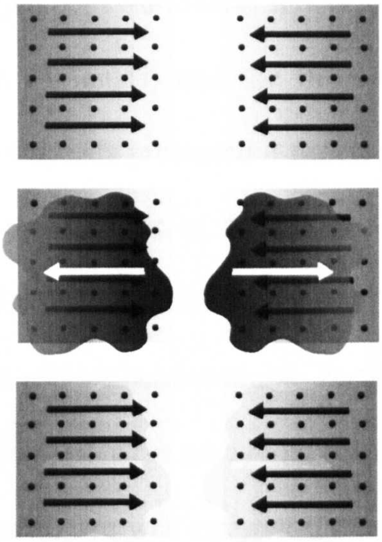


Fig 1: Diagram to illustrate the technique employed. Following exposure to motion for a period of time, an after-effect (as measured by direction) should for a period of time dominate the observer's perception. Due to the presence of the test speed, the after-effect should gradually decrease as it is being nulled by the presence of the test stimulus. Our measure of the after-effect strength and magnitude is taken from sampling change in the perception of direction of motion over time, and with different test velocities.

By manipulating the velocity in the test stimulus, the amount of time taken for the after-effect to dissipate should vary, giving a measure of the change of the adaptation mechanism that can be correlated with time. The exact relationship between change of velocity and decay of the after-effect is unclear though, and unlike the previous work on disparity mechanisms (O'Kane & Mamassian, 2003, VSS Abstract and Chapter 3), may not be linear (Pantle, 1998). A comparison of the type of decay function is addressed.

4.3.2 Design

This experiment had two independent variables: the velocity of the test speed presented following adaptation (4 levels) and the time at which the response occurred (8 levels). There were 4 speeds presented 4 times, giving 12 trials in total during the testing period. The presentation of the test speeds was random. The stimuli were displayed on a SONY 21" Trinitron monitor. The participant's head position was maintained constant using a head restraint. Participants were seated at a distance of 75 cm from the screen and wore an eye patch over one eye during the course of the experiment. The same eye was covered throughout the course of the experiment. The observer made no response during the first 20 seconds of the experiment. They then made a forced choice response (left or right wards motion) at an interval occurring on average every second when they heard a beep. The direction of the motion changed for each trial adaptation to counteract build up of the effect. In order to keep eye movements at a minimum, mirrored movies were presented simultaneously, depicting either 'inwards' or 'outwards' motion.

4.3.3 Stimulus

The stimuli were generated on an Apple Mac G5 using the psychophysics toolbox in MATLAB (Brainard, 1995; Pelli, 1997). A textured, patterned surface was generated and placed on a surface subtending 4 degrees of visual angle. This gave a dot size of 11.52 arc min of diameter and an overall dot density of 5.7 dots per square degree. The peak luminance of the screen was 72.4 cd m^{-2} giving an average luminance of 36.2 cd m^{-2} . A movie of the dots was generated for both the adaptation and test phase of the experiment. The speed of the dots during the adaptation was maintained constant at a speed of 3.9 °/sec. The average displacement during the adaptation phase was 2.5 pixels per frame. When one dot disappeared it was wrapped around on the other side of the stimulus in order to maintain continuity of movement. The dot colour varied between 0 and 255 in brightness. The dots moved with a displacement of 10%, 20% and 30% of the adapting stimulus during the testing period (giving a speed of 0, .39, .78 &1.17 °/sec respectively). The contrast of the adaptation stimuli was 1, and the contrast of the test stimuli was presented at a slightly decreased level, .95. Contrast was defined as the maximum luminance in the image minus the minimum luminance, as a proportion of the average luminance.

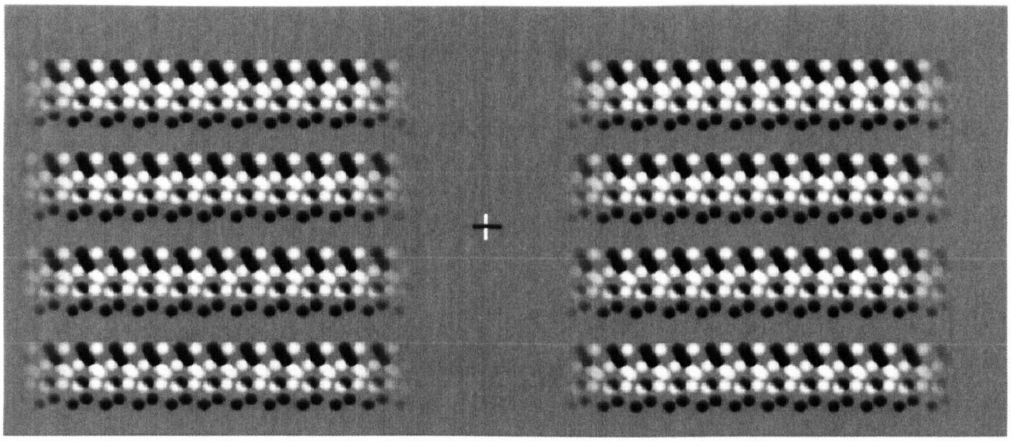


Fig 2. Single frame of the adaptation and test stimulus used for testing the MAE. Participants were presented with a stimulus that was moving either 'inwards' or 'outwards'. The following test stimuli were different only in the amount of velocity they contained.

4.3.4 Participants

There were five observers in this experiment. All were naïve to the purpose of the experiment apart from the experimenter (LO). Participants LO, TC, EC had corrected to normal vision. All except one observer (IR) were experienced psychophysical observers. All were paid for their participation in this experiment.

4.3.5 Procedure

Participants adapted to motion (inwards or outwards) for a period of 20 seconds (see Figure 2). Following adaptation, a brief test stimulus (duration .26sec) was presented repeatedly every second with a small temporal jitter occurring randomly on every test trial. The test stimuli were similar to the adaptation stimulus except that they had a fraction of the adapting speed (which could be one of four different values, varying from 0 to 30%) and were presented at a slightly decreased Michelson contrast (.95). They therefore differed in that they were slower than the adaptation stimuli. A visual depiction of the time course of the experiment is illustrated in Figure 3. Figure 3 depicts the change in the visual presentation of the stimulus from constant through the first 20 seconds of the experiment, changing to intermittent presentation of stimuli during the testing period.

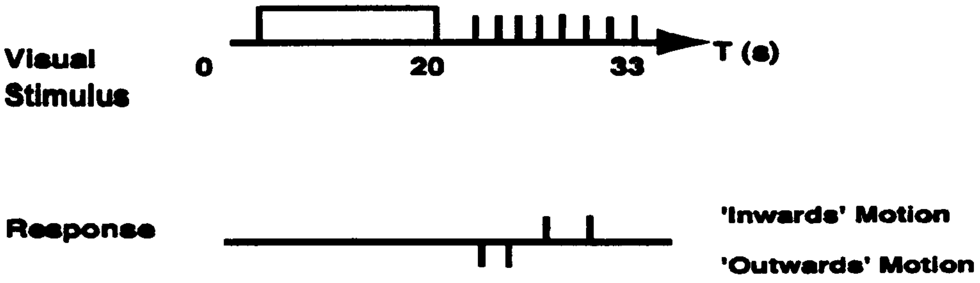


Fig 3: Time course of experiment. Participants observed the moving stimuli for a period of 20 seconds.

4.3.6 Analysis

The individual data for each observer were fitted with the complement Gaussian function. The initial aim was to extract the PSE value as this number would corresponds to the amount of time it takes for the test stimulus to appear equally in one direction as another. However, the data for most observers did not cross the .5 threshold, indicating that the speeds used in the experiment were above the threshold for obtaining a reversal of motion. In this instance, the tangent to the point of inflection on the fits for each observer was taken as a measure of the time constant of the after-effect. Analysis revealed that the time course for the static condition differed substantially from any of the moving tests (dynamic). The data were then combined for all observers and an ANOVA performed on the means for all the data.

4.4 Results

The individual results obtained for this experiment for five subjects are illustrated in Figure 4.

The after-effect strength is taken as the proportion of times the observer responded in the direction of the after-effect at each time interval measured. A 2 factor (Time by Velocity) repeated measures ANOVA was performed on the means across repetitions obtained in the experiment. Two main effects of velocity and time were found to be significant: $F(1,4) = 16.761$, $p<,.015$ and $F(7,28) = 2.809$, $p<.024$ respectively.

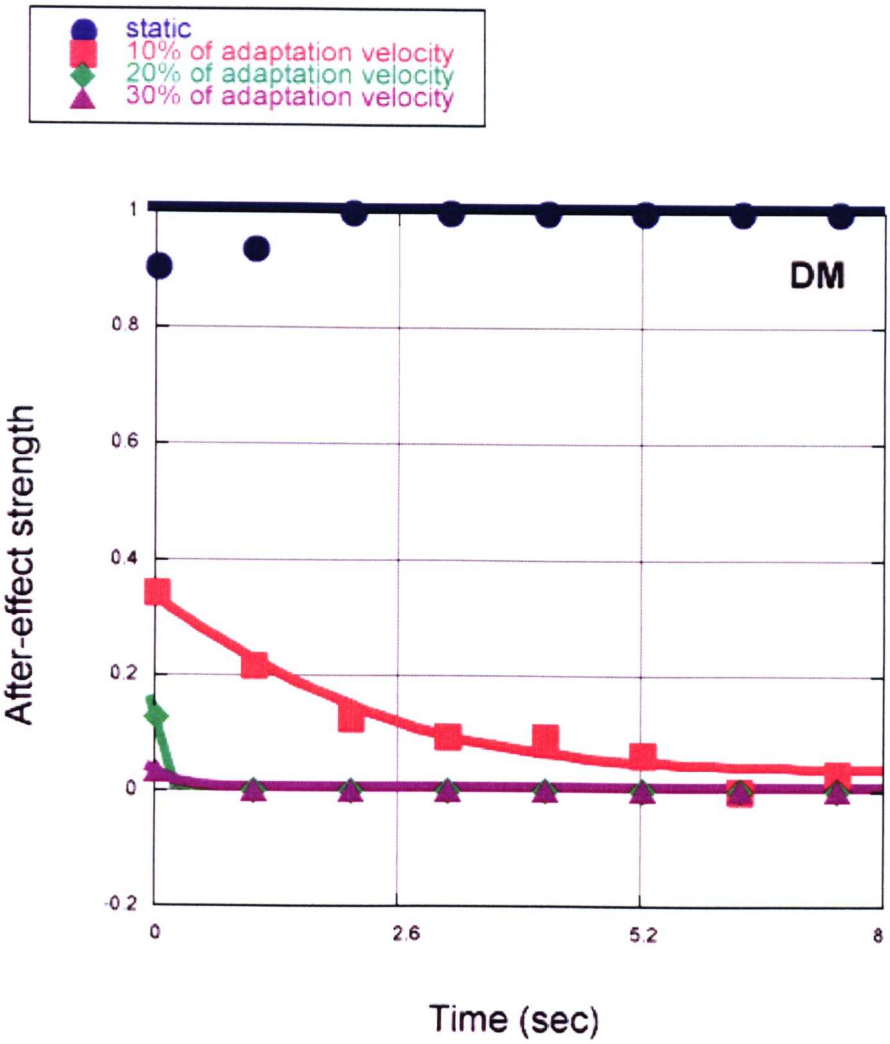


Fig: 4(i). Observer DM. Proportion of times test stimuli was perceived to be moving in the direction predicted by the after-effect, which is taken as our measure of after-effect strength. Each curve represents a different test velocity.

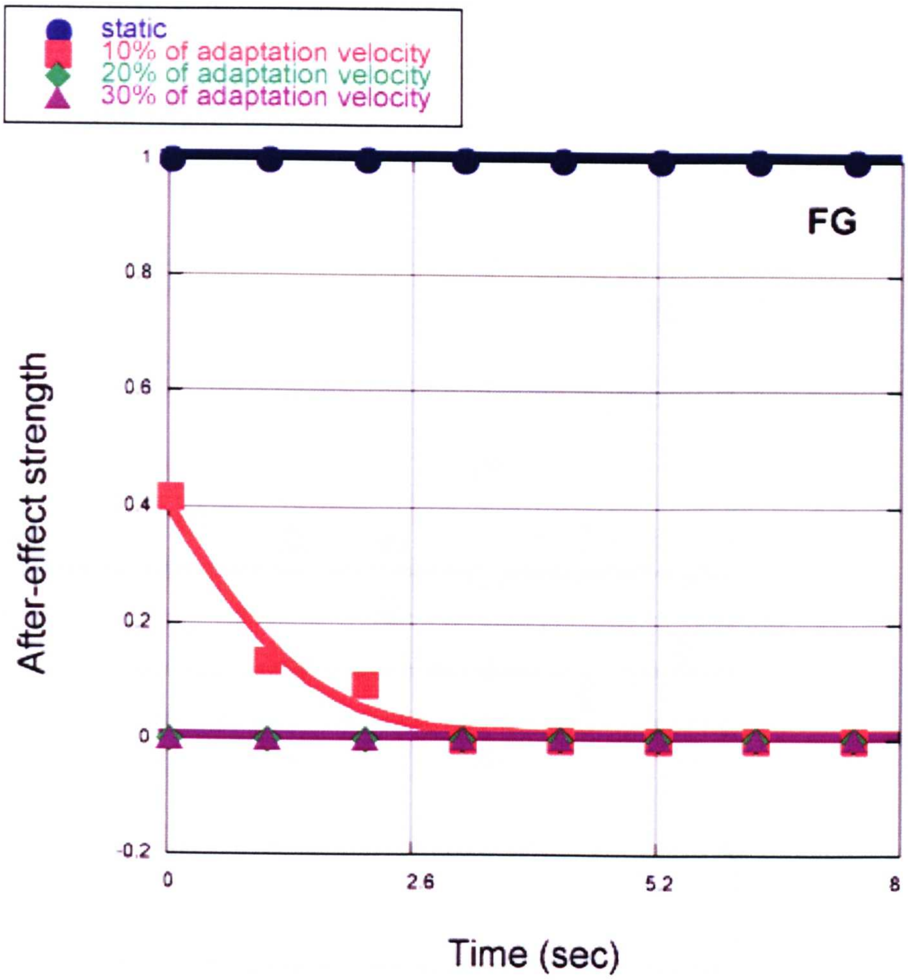


Fig: 4(ii). Observer FG. Proportion of times test stimuli was perceived to be moving in the direction predicted by the after-effect, which is taken as our measure of after-effect strength. Each curve represents a different test velocity.

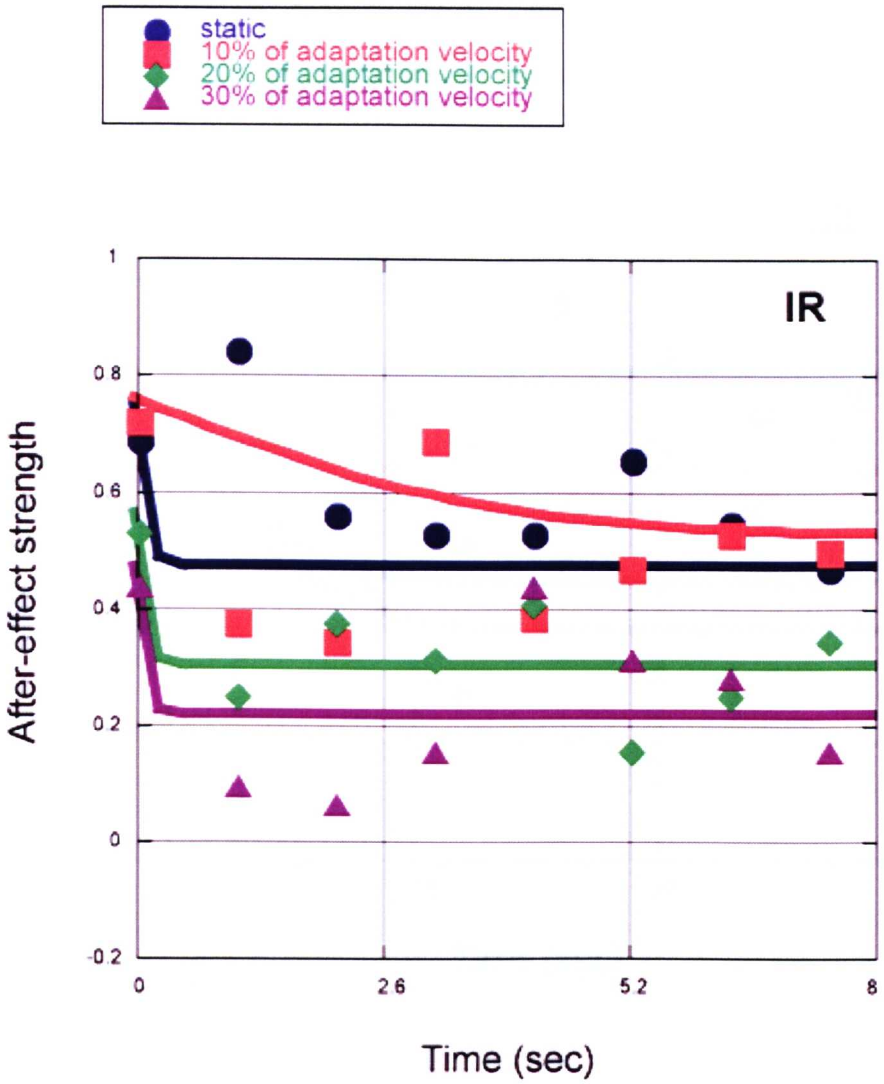


Fig: 4(iii). Observer IR. Proportion of times test stimuli was perceived to be moving in the direction predicted by the after-effect, which is taken as our measure of after-effect strength. Each curve represents a different test velocity.

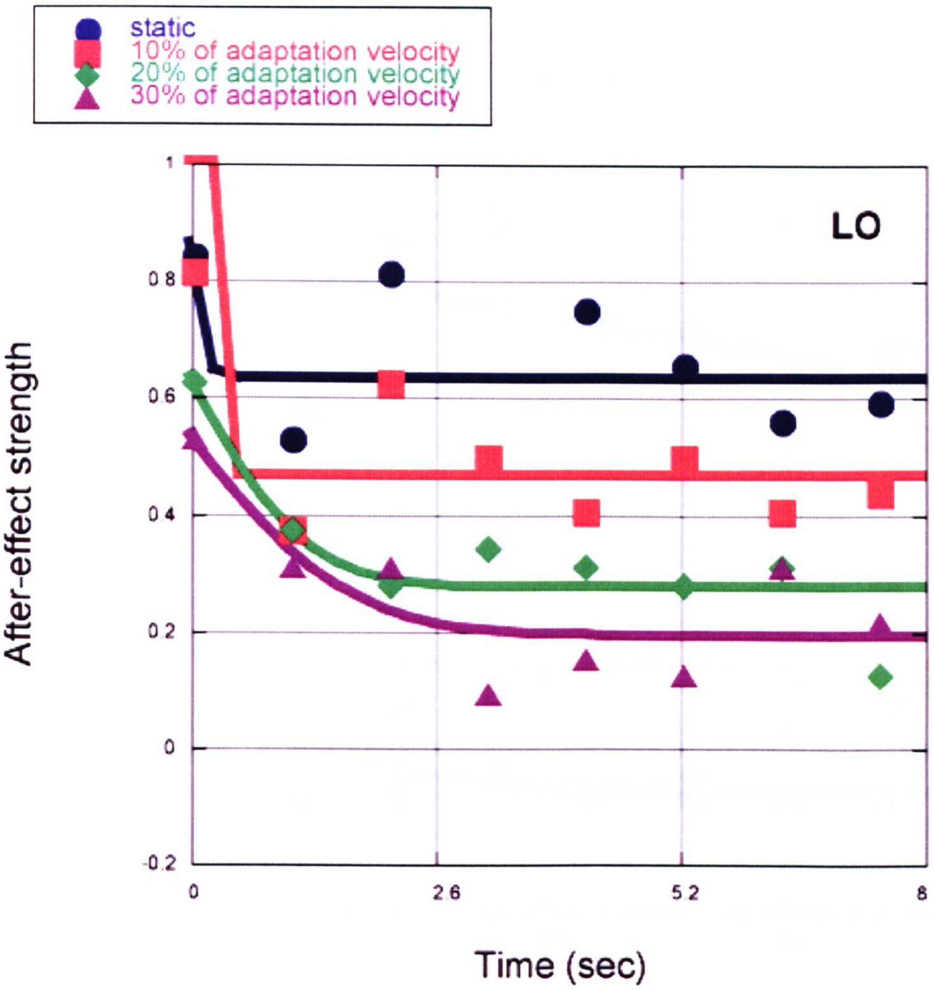


Fig: 4(iv). Observer LO. Proportion of times test stimuli was perceived to be moving in the direction predicted by the after-effect, which is taken as our measure of after-effect strength. Each curve represents a different test velocity.

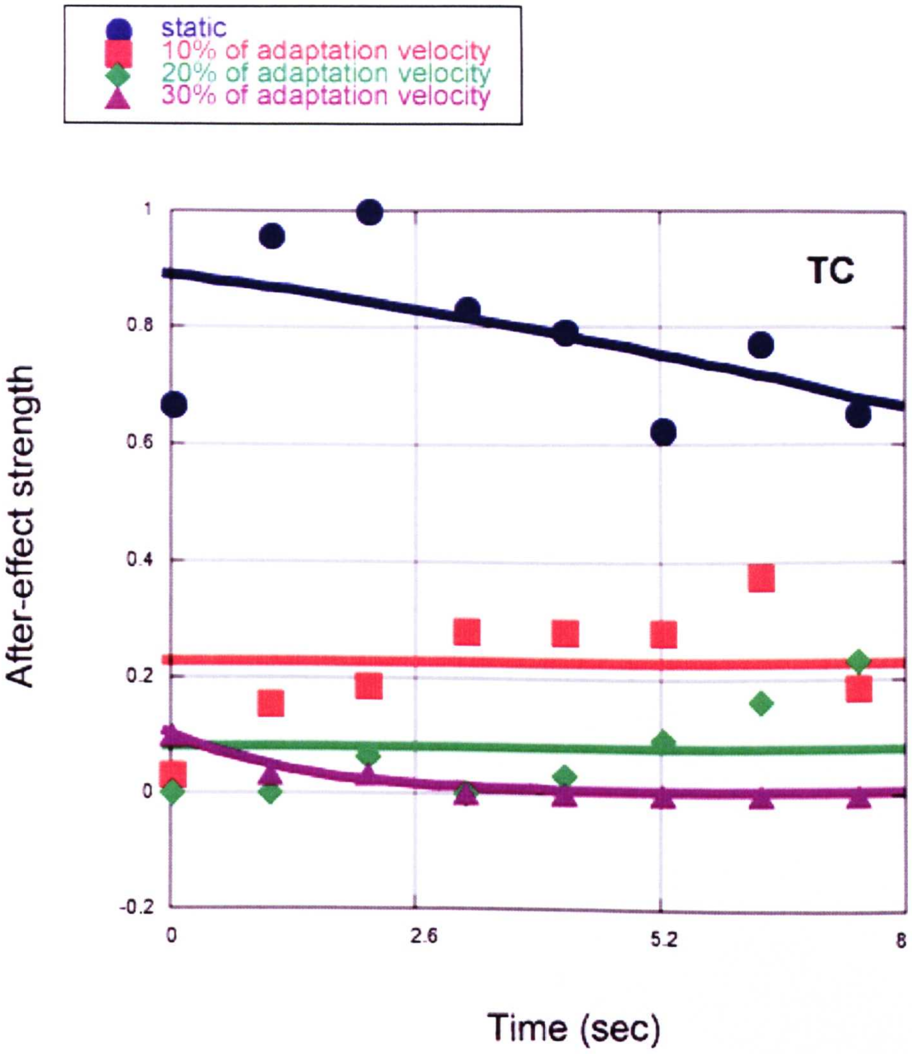


Fig: 4(v). Observer TC. Proportion of times test stimuli was perceived to be moving in the direction predicted by the after-effect, which is taken as our measure of after-effect strength. Each curve represents a different test velocity.

It can be seen from Figure 4(I-V) that, as the test speed increases, the proportion of times the observer responded in the direction of the MAE decreases, excluding the static condition. For the static condition, we cannot address how the after-effect varies with time, but just when it ends. The top line of the graph illustrates the dissipation of the after-effect with the presentation of a static test stimulus. The lower fits reflect the dissipation of the effect with increasing velocity present in the testing sequence. This was tested over a range between 10 and 30% of the adaptation velocity for all observers. The testing period lasted 8 seconds in total.

For all observers, as the velocity in the test stimulus increases, the estimated time constant of the after-effect decreases. The time constant is largest for the static test, and decreases sharply with increasing test speed.

The data averaged for all observers is included in Fig. 5. This demonstrates the mean after-effect strength for all observers across (a) test velocity used and (b) test velocity at each time interval measured. This shows the strength of the after-effect (as we define it) for all the data obtained for each speed and test interval measured.

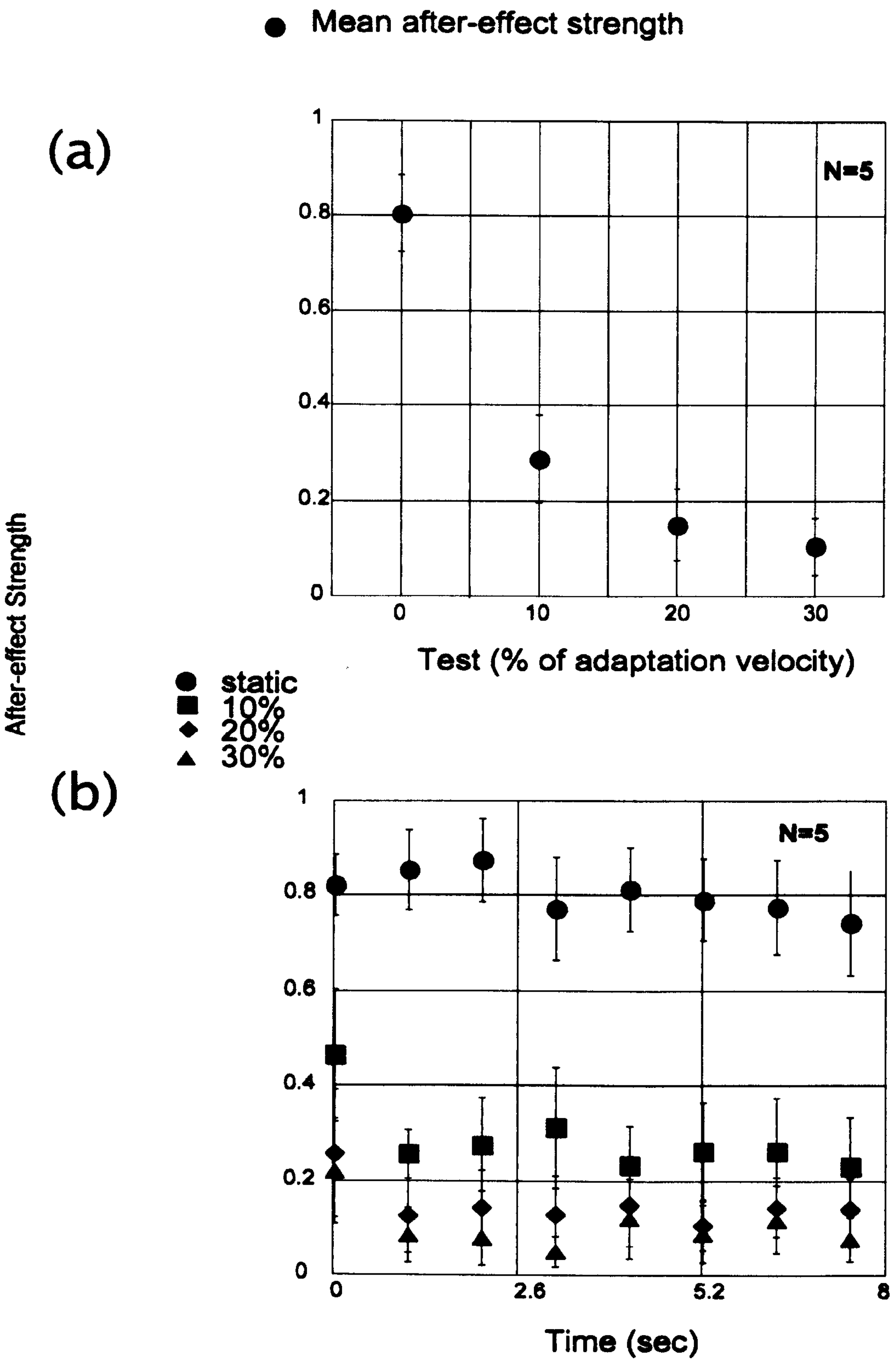


Fig. 5 Graphs to show mean after-effect strength for all participants acros test velocity (b) velocity across time

The data presented here attempted to measure the temporal variation of the MAE over a range of test stimuli that vary in velocity. This differs from other data obtained in previous experiments as it shows the duration and magnitude of the effect as it varies with time for the MAE using both a static and moving test. However, for the values tested here for each participant, a PSE value could not be obtained which is critical to the technique that we are applying. In order to achieve this, different speeds would need to be tested. This is one of the aims of the next chapter (chapter 5).

4.5 Discussion: Time Course of After-effect

4.5.1 Duration

Hershenson (1993) reported that the duration of the MAE showed a square root dependence on adaptation time. Extrapolating from the data presented in Figure 2 of that paper predicts a duration of just over 16 seconds for a 20 second adaptation time. Despite the differences in adaptation pattern and speed this estimate is consistent with the long-lasting MAE found with the static test. However, with all the non-static test patterns the after-effect declined sharply within the first few seconds and reached an asymptote within the first 8 seconds. Time constants (taken as the tangent to the inflection point for the fits in Fig 4) for the moving test patterns ranged from -3 to 4.4 seconds. The time constant tended to decrease with increasing test pattern velocity. The one negative value obtained occurred for one participant and this was the experimenter (LO).

4.5.2 Magnitude

Whilst it was impossible to measure the MAE with a static test in this way, the total number of responses in the after-effect direction during the test period can be compared. These data, averaged across the five observers, are illustrated in Figure 5. It can be seen that, as with the duration data, the after-effect is very strong with the static test (80 %), but reduced with the dynamic tests. The magnitude decreases with increasing test speed. The effect is a velocity after-effect (Thompson, 1981) however as our index was direction (and not perceived speed), we are attempting to measure the motion after-effect.

4.5.3 Different Test Structures

The most striking result to emerge from these experiments was the difference in the strength and temporal dynamics of the MAEs obtained with static and dynamic tests. With the static test, responses in the after-effect direction persisted throughout the test period. In fact, during de-briefing participants reported surprise that in one condition (which was the static test, although they were not aware of it) they always perceived motion in the same direction, and were worried that there was a problem with the stimulus! With the dynamic tests, although there was an initial response in the direction of the aftereffect this quite rapidly disappeared, even when the speed of the test was relatively slow (4% of adaptation speed). The time course of the decay in the after-effect was quite similar at all the dynamic test speeds, although the precise rate of decay varied with test speed (see Fig. 5a).

This result supports the notion of a distinction in time course between static and dynamic motion after-effects (Nishida et al, 1994). It has been suggested that the two kinds of MAEs may reveal different stages of motion processing (Nishida & Sato, 1995) with the processing of dynamic tests reflecting a higher, integration stage of motion processing. For example, typically, the dynamic MAE is affected by such factors as interocular transfer and attention, whereas the static after-effect is not (Nishida & Ashida, 1999).

Many differences have been found between the after-effect elicited by static test and dynamic tests. Use of a static test when measuring the MAE shows spatial frequency selectivity (Over, Broerse, Crassinu & Lovegrove, 1973; Cameron, Baker & Boulton, 1992) and differences between responses to first- and second-order motion (Derrington & Badcock, 1985). With the dynamic test there is no spatial frequency selectivity (Ashida & Osaka, 1994) and the magnitude of the after-effect is dependent on the speed rather than the temporal frequency of the adaptation stimulus (Ashida & Osaka, 1995). If a combination of adaptation motions including both first order and second order components is included, then the static motion after-effect is found to be opposite to the first order component and the dMAE is found to be opposite to the second order component (Nishida & Sato, 1995).

With the static test, the perception of motion appeared to be completely stored throughout the testing period, whereas the after-effect obtained using moving test stimuli decayed sharply. In previous studies a counterphase grating was utilised (Mather & Verstraten, 1998). Here we used a stimulus drifting in the same direction as the adaptation stimulus, but at a fraction of the velocity.

A possible advantage of this technique is that it measures precisely how the differences in after-effect magnitude obtained with static and moving tests vary with time. Other studies have proposed differences in the two types of after-effect elicited by static and moving (dynamic) test stimuli (Verstraten, 1996). This study supports this view by demonstrating that when an observer's percept is tracked over time, the perception shows a remarkably different time course dependent on the test structure. However, an important point is that in the current study the test stimulus that was moving was not directionally ambiguous, except in the effect that the MAE was having on the observer's perception. This is different from the use of dynamic test stimuli in research regarding the MAE, where the type of test, for example counterphase gratings, is directionally ambiguous. We therefore cannot generalise these results to conclude that the dynamic and static after-effects demonstrate a different time course, but we can conclude that there is a difference in the after-effect obtained when there is movement present in the test stimulus as compared with static. If two sub-populations of temporally tuned motion detectors underly the difference between static and dynamic after-effects as has been proposed, then it is possible that the differences in decay obtained using a movement test are due to the activation of the sub-population of units tuned to higher speeds.

There is also a differential effect of storage on the perception of the after-effect. Whilst this had been proposed (Verstraten, 1996) however this data contributes a demonstration on the actual time course of the difference obtained when using a static and moving test. Application of this technique allows a psychophysical complement to the physiological studies that are focused on studying the time course of adaptation (e.g Hammond et al, 1988).

One possible argument is that, as the test stimulus was briefly flashed during the test period this may have induced motion priming effects (Kanai & Verstraten, 2005), where the perception of motion in the same direction as the test is enhanced. However, comparing the precise timing of our stimulus (260 ms with abrupt onset and offset with a 1 sec ISI) with that of Kanai & Verstraten (2005) suggests that this was unlikely to have reduced the strength of the motion after-effect, and may in fact have slightly enhanced it.

4.6 Summary

This experiment has attempted to look at the temporal dynamics of the motion after-effect. It was found that the perception of the after-effect was affected both by the velocity of the test stimulus and the time at which the test occurred.

With further experiments including a larger data set, the exact relation between velocity and perception of the MAE could be established.

The difference between the presentation of a static and dynamic test is reflected in the perceived decay of the after-effect. This is a disputed area, and the present findings contribute to the understanding of the differential processing of the effect. In particular, whilst it is generally acknowledged that different aftereffects exist, it has not previously been demonstrated that they have different temporal dynamics. Theoretically, this supports the existence of two types of after-effects perhaps elicited by different test stimuli.

In summary, the data presented here attempted to measure the temporal dynamics of the MAE over a range of test stimuli that vary in velocity. This differs from other data obtained in previous experiments as it shows how the duration and magnitude of the effect as it varies with time for the MAE. However, for the values tested here for each participant, a PSE value could not be obtained which is critical to the technique that we are applying. In order to achieve this, different speeds would need to be tested. This is one of the aims of the next chapter (chapter 5).

The next step in the present research is therefore to create an adaptation and test stimulus that can be used to stimulate both adaptation sites optimally, in order to obtain the strongest motion after-effect to give the best chance of capturing the full temporal dynamics of the after-effect. An improvement in the strength of the after-effect may be found if a different stimulus was used, for instance a Gabor patch. The next experiment using this stimulus is described in the Chapter 5.

This chapter provides two key points of interest. First, we rigorously test the technique developed in the previous chapters. We provide further evidence that the technique is a robust measure of magnitude and duration of an after-effect, which can be used with inexperienced psychophysical observers. This provides supporting evidence of the utility of this technique as an estimate of after-effect magnitude, duration and strength at time zero.

We also investigate the relation between adaptation and test stimuli velocity in the recording of the MAE. This is critical because, as outlined in Chapter 2, current theoretical accounts of adaptation are derived from research revealing a complex relationship between adaptation and after-effect, that is difficult to explain by fatigue or saturation mechanisms alone (Thompson, 1998).

A critical factor in such studies is the similarity between adaptation and test (Clifford et al, 2005). Here we report the changing temporal characteristics of the MAE using an adaptor and test which differ in velocity. Using the current technique, adaptation to a high-speed stimulus gave rise to a perceptual reversal with a low speed test. This has implications for theoretical attempts to explain differential motion adaptation results in terms of velocity tuning of neurons.

5.1 Introduction

In the previous chapter we developed a technique for capturing the temporal dynamics of the MAE. However, the strength and magnitude captured in this instance was relatively weak. A consideration was that in order to access the full temporal variation of the after-effect it might be necessary to generate a stronger and longer lasting after-effect. We therefore sought to fully capture the temporal dynamics of the motion after-effect using a different stimulus during adaptation.

This experiment utilises the same technique applied in the previous chapters. Four changes were made so as to induce a longer lasting after-effect. The stimuli were changed to purely "first order" stimuli (drifting sinusoids in Gaussian windows) (ii) the adaptation time was increased (iii) the eccentricity of the stimuli was increased and (iv) only dynamic stimuli were used in the testing period. First order motion is motion that is defined by luminance change. It can be compared with second order motion where the contour is defined by contrast, texture or flicker but not an increase in luminance energy.

We predict that by utilising this technique this modified design would result in a stronger proportion of responses perceived in the direction of the after-effect, and the time to reach the point of subjective equality should be increased. Furthermore, due to the complex nature of the relationship between adaptation and test interaction that has been found when researching the MAE (see Pantle, 1998) this experiment provided an opportunity to investigate how the temporal dynamics of the MAE change with differences between adaptation and test.

Previous results supporting a ratio model of velocity coding (e.g Wright & Johnston, 1985) have cancelled the MAE using a drifting grating moving in the same direction as the adaptation stimulus, similar to the study presented here. However, in this study we record the reversal of the perception of motion from the direction specified by the after-effect moving back to that specified by the true motion signal over time.

Initial predictions with the current technique were that a perceptual reversal would be obtained when adaptation and test which were similar. Related to this prediction is the proposal that there is a difference between high and low speed systems (van der Smaagt, 1999; van de Grind, 2001, Verstraten, 1998) a finding that could potentially underlie differential results obtained from motion adaptation studies.

The key finding is that two different after-effects can be found relating to the type of test stimulus used, and this has also been linked to the velocity of the test. The type of MAE test used (static or dynamic) not only exhibits differences in storage and duration, but also in the effect revealed by different speeds. Verstraten et al (1996) use differences in MAE duration obtained under different test conditions to support the distinction of two mechanisms, exhibiting different storage characteristics for static and dynamic tests. This has then been linked to the finding that static MAE's are predominant at low speeds while dynamic MAE's are dominant at higher speeds (Verstraten, 1998).

This has led to the suggestion that there are high and low speed systems represented in populations of cells with different temporal tuning characteristics. This has originated from the fact that differences in after-effects are found following adaptation to the type of speed used. Evidence that there is independent coding of these two systems comes from the finding that if two speeds are adapted to, one fast and one slow, a two component motion after-effect (appearing transparent) can be created (van der Smagt, 1999). This suggests that there are two independent channels of motion being coded, because if this was not the case, then one motion after-effect (perhaps at a combined speed of the adapting stimuli) would be expected.

In preliminary results in the present research this effect was not found for a range of test stimuli closely related to the adaptation stimuli. So for example, when testing with an adaptation stimulus of 22.5deg/sec and a test of 20deg/sec, no after-effect was observed. However, a reversal was found when the speed of the test stimuli was varied. For all observers, a perceptual reversal was found when testing with a slow speed relative to the adaptation speed was used. Theoretically this is intriguing as using the logic put forward by others (e.g Castet, Keeble & Verstraten, 2002) the use of a dynamic test stimulus preferentially reveals the adaptation of a population of high speed motion units whose activity is independent of adapted low speed units.

We report a perceptual reversal obtained using a high speed adapting stimulus and a slow moving test.

Complex relations have often been described when looking closely at the MAE. A strong example of this is examination of the interaction between contrast and recording of the MAE. Nishida et al (1997a) examined the effects of contrast on a range of static and dynamic tests. They demonstrated that the strength of the MAE saturated with a low contrast, but not with a high contrast test. This has been used to argue against a fatigue process underlying the MAE.

The present study also presents findings demonstrating the complex relation between speed of adaptor and test as revealed by the application of this technique. This finding has relevance for theoretical models that dissociate between high and low speed units in the underlying mechanisms of adaptation. Our hypothesis is that as test speed increases, the time taken for the after-effect to decay will increase and we are interested in measuring the temporal variation of this decay.

5.2.1 Methods

Apparatus

Images were presented using a G4 computer on a Sony 21" Trinitron monitor (75hz). We used standard anti aliasing techniques. The spatial resolution 1024 by 768. Participants sat with their head in a headrest positioned at 57.3 cm from the screen. As the experiment was monocular, participants viewed the images whilst wearing an eye patch over one eye. We did a gamma correction for the luminance values, such that luminance increased linearly with grey value. The mean luminance of 31.3cd/m^2.

Stimuli

Images were generated using the psychophysics toolbox for MATLAB (Brainard, 1997; Pelli, 1997), firstly by generating a Gabor patch and displaying this on the screen. To create the movement in the stimuli, this was then moved at a fixed number of pixels per frame. To keep eye movements at a minimum, the movie was then placed on half the screen and an opposite but identical image presented on the other half of the screen.

The images were placed at eccentricity of 11.86 °. At a viewing distance of 57.3 cm, the images had a spatial frequency of .333 cpd and the Gabor had a Gaussian envelope with a standard deviation of 2.25 degrees. The contrast of the images was 1. The temporal frequency of the stimuli was 7.5hz, which is in the middle of the maximum after-effect range (6-10hz) reported in a study investigating the temporal frequency tuning of the motion after-effect (Wright & Johnstone, 1985).

The stimulus was displayed for a total time of 78 seconds (see Fig. 1). After the first 48 seconds, the speed of the image was changed to a slower speed, which was blocked throughout the experiment (see Fig. 2: time course of the experiment). The speed of the stimuli during the first 48 seconds was constant (22.5°/sec). During the testing phase, there was one of three test speeds (1% (0.225deg/sec), 3% (0.675 deg/sec), or 4.5% (1deg/sec)) presented. For each test speed presented, this lasted for the full 30 seconds of the testing period.

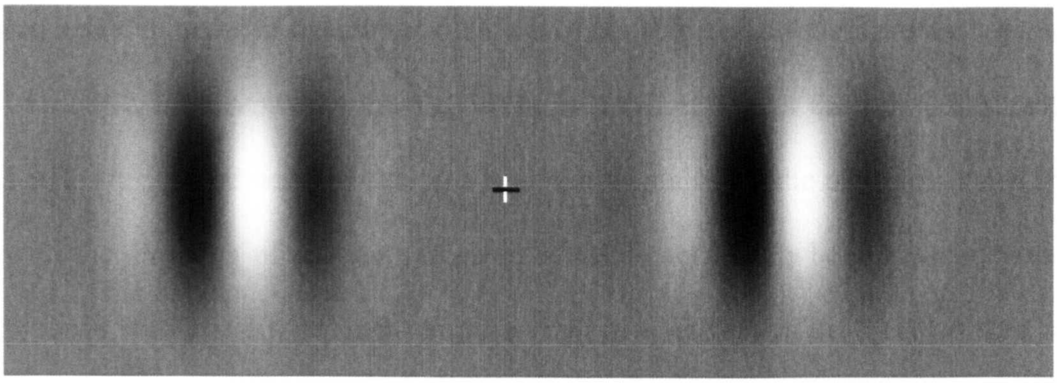


Fig. 1. Single frame of stimulus used in the experiment. This was identical between adaptation and test, but varied in the velocity at which it was presented at. During adaptation the speed was high and during the testing phase the speed was slow.

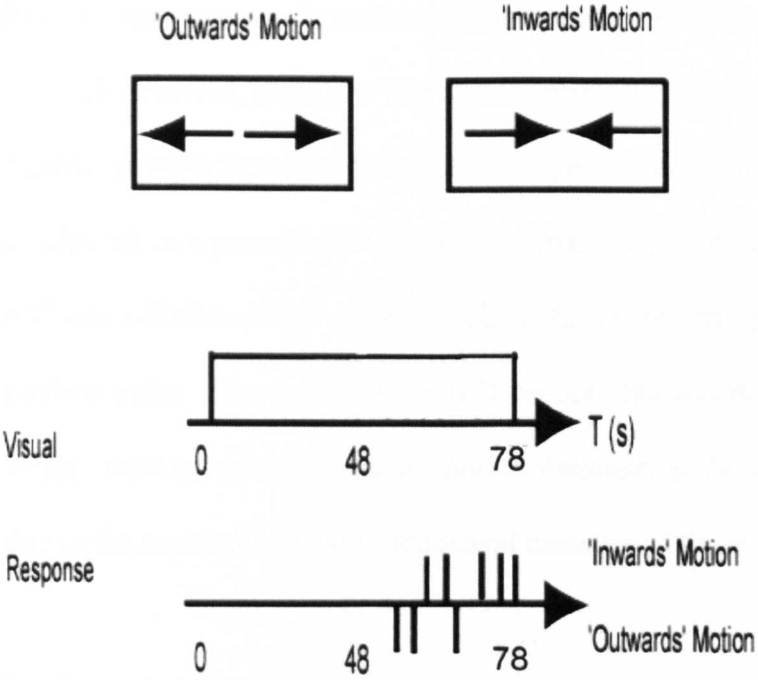


Fig 2. Depiction of time course of experiment. For 48 seconds participants adapted to one direction of motion, either 'inwards' or 'outwards' on the screen. The test was always moving in the same direction of motion as to that which was adapted to, however, perceived direction was recorded over tests which varied between 1.5%, 3% and 4.5% of the adaptation velocity. When the adaptation period ended, participants were required to press a key on average every 2 seconds indicating the perceived direction of motion. The perception of motion in the opposite direction to that which was adapted too was taken as a measure of the after-effect.

The direction of motion was alternated with every combination of trial and test sequence, in order to counteract build up of the effect. However, the testing stimuli were always presented as moving in the same direction as the adaptation motion. The testing period was marked by a beep that signalled to the participant to respond with the direction of motion perceived in the images. This beep occurred every 2 seconds with a slight random temporal jitter around that value. This resulted in 15 responses for each testing period on average.

Procedure

Participants were run on each combination of adaptation +test speed 16 times. Thus for each observer, there are 16 points contributing to the perception of direction of motion at each time slot for each test speed used. The test speed presented was conducted in a pseudo-random order. First, the participant was tested to obtain an estimate of after-effect strength. Then the other test speeds were presented in a random order. Due to individual differences, this was done to ensure that the after-effect could cause a reversal of motion direction at the particular speeds presented due to the reversal being our dependent measure of the after-effect.

Each combination of adaptation and test speed was presented as a separate experimental session. In each session 4 blocks were presented. Each block consisted of 120 2AFC task trials, in which the test speed was kept constant at the value selected for that experimental session. The participants' task was to judge the direction of motion in the temporal interval. Participants were given these instructions verbally prior to the start of the experiment. The response was recorded via a key press. Each session lasted 21 minutes and a minimum of 3 sessions were run for each condition, giving 6 blocks in total for each condition. Each participant carried out a minimum of 720 trials.

Participants

Six participants took part in the experiment. All had normal or corrected to normal vision. All were naïve apart from the experimenter (LO).

Analysis

The analysis presented here is similar to the one presented in Chapter 3 & 4. First, we report the proportion of times participants responded in the direction predicted by the motion after-effect for each test speed at each time point following the end of adaptation period. Individual data are fitted with a decreasing cumulative Gaussian function to obtain an estimate of the PSE for each test velocity. This measure is then taken and a linear regression analysis is performed to give an estimate of the initial velocity required to null the after-effect. The data are also combined and a 2 way within subjects ANOVA performed. Post hoc analysis is also presented.

5.2.2 Results

The individual data for each participant is illustrated in Fig. 3(I-VI).

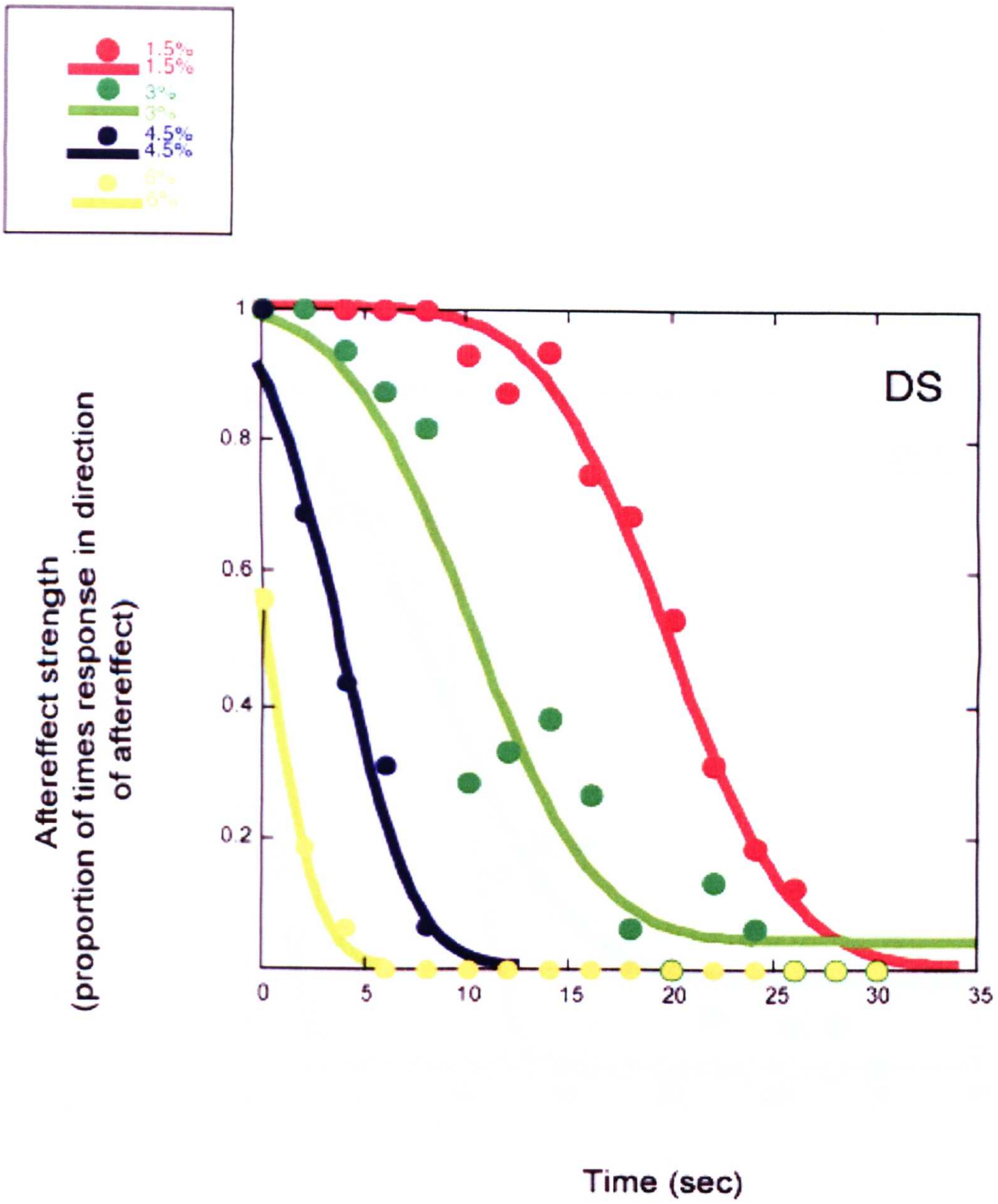


Fig 3 (i). *Proportion of times the observer responded in the direction consistent with a motion after-effect. Each curve represents a different velocity used in the test stimulus.*

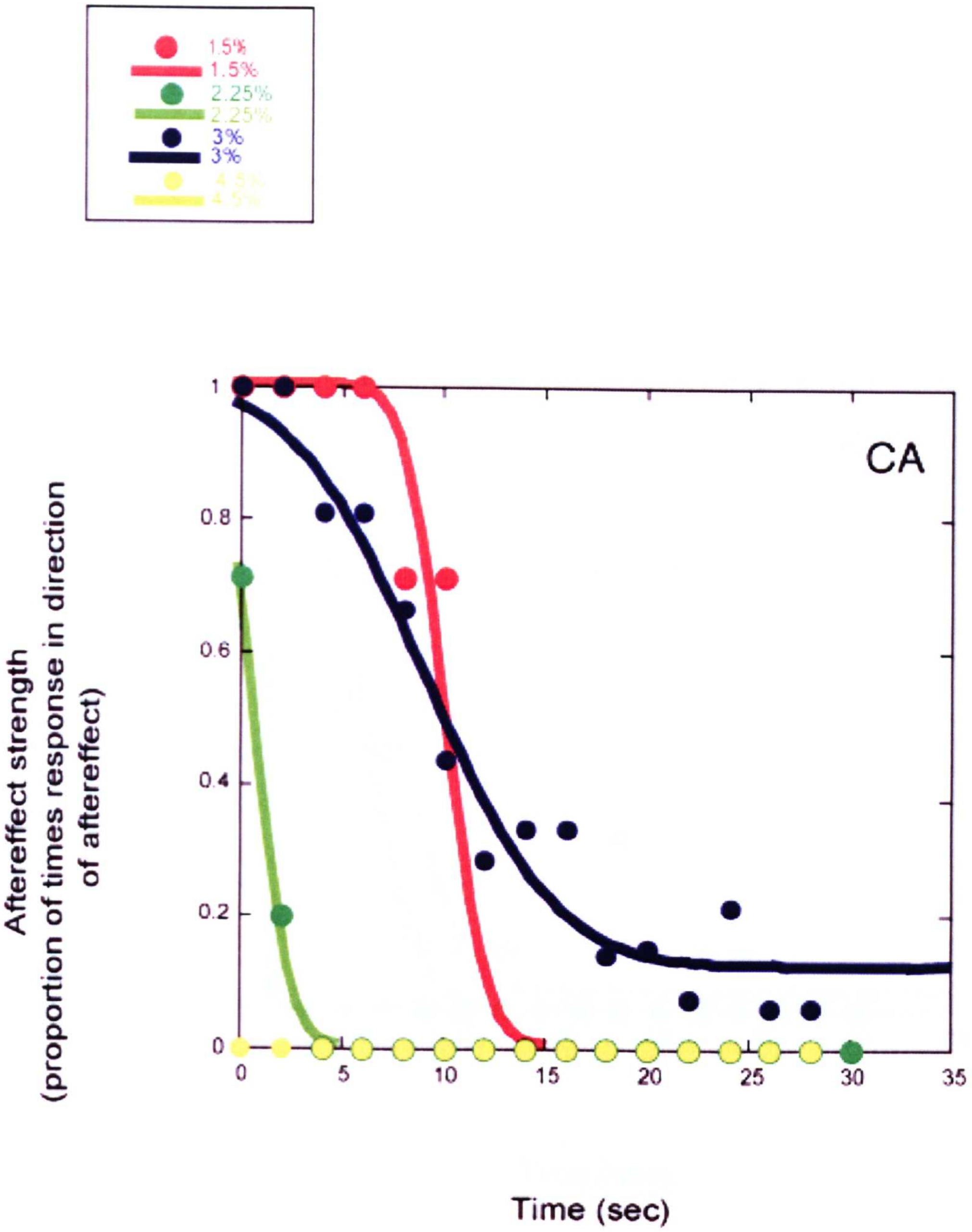


Fig 3 (ii). *Proportion of times the observer responded in the direction consistent with a motion after-effect Each curve represents a different velocity used in the test stimulus.*

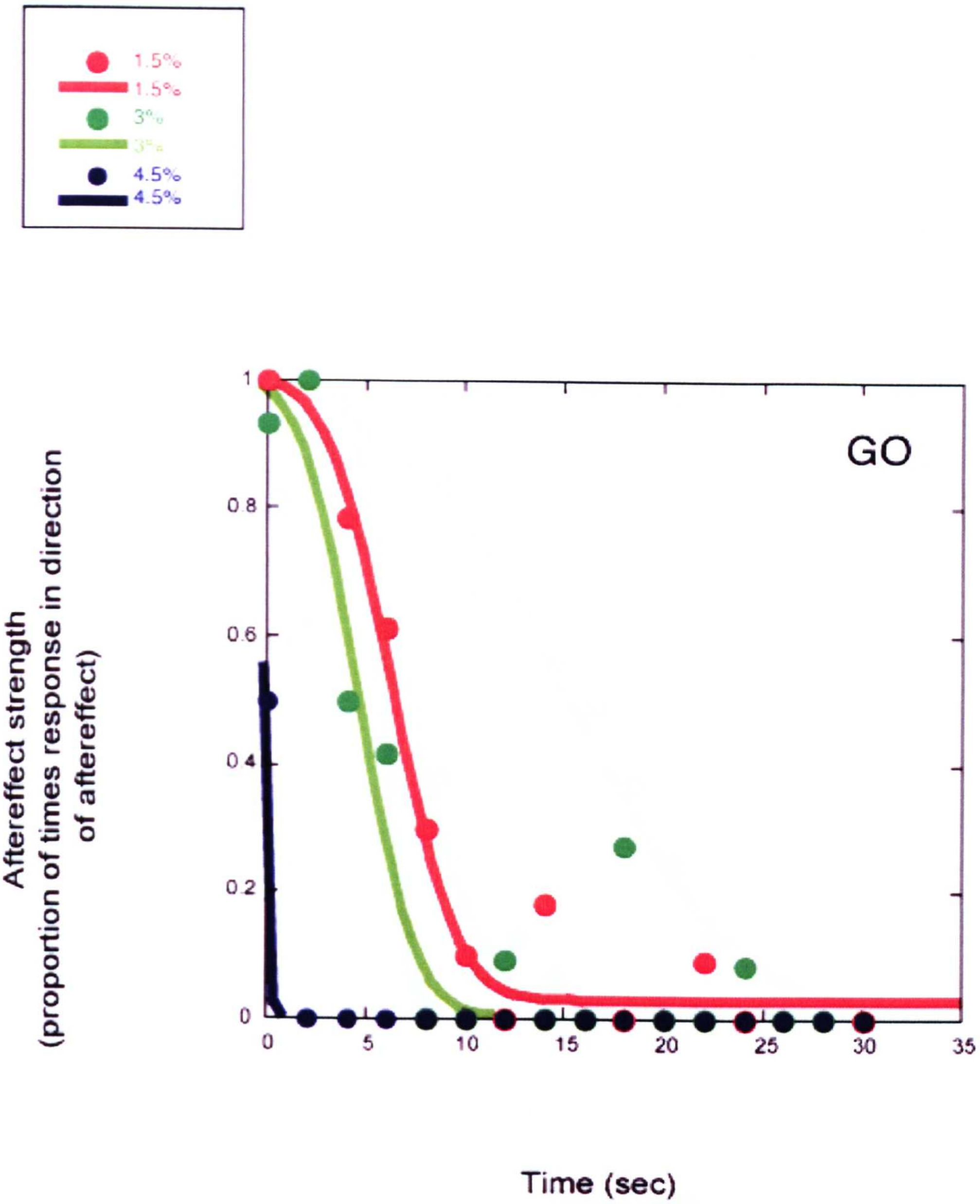


Fig 3 (iii). *Proportion of times the observer responded in the direction consistent with a motion after-effect. Each curve represents a different velocity used in the test stimulus.*

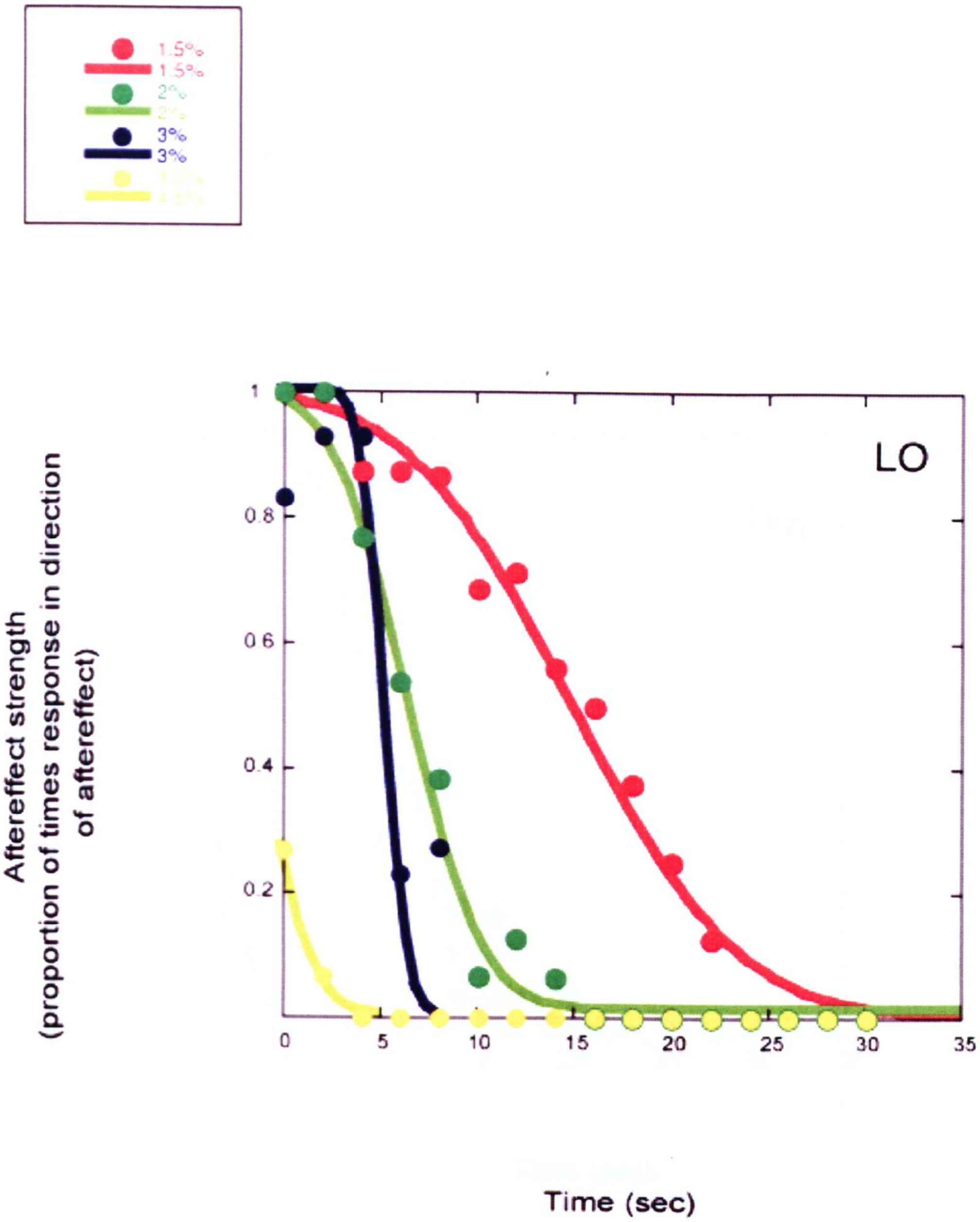


Fig 3 (iv). *Proportion of times the observer responded in the direction consistent with a motion after-effect. Each curve represents a different velocity used in the test stimulus.*

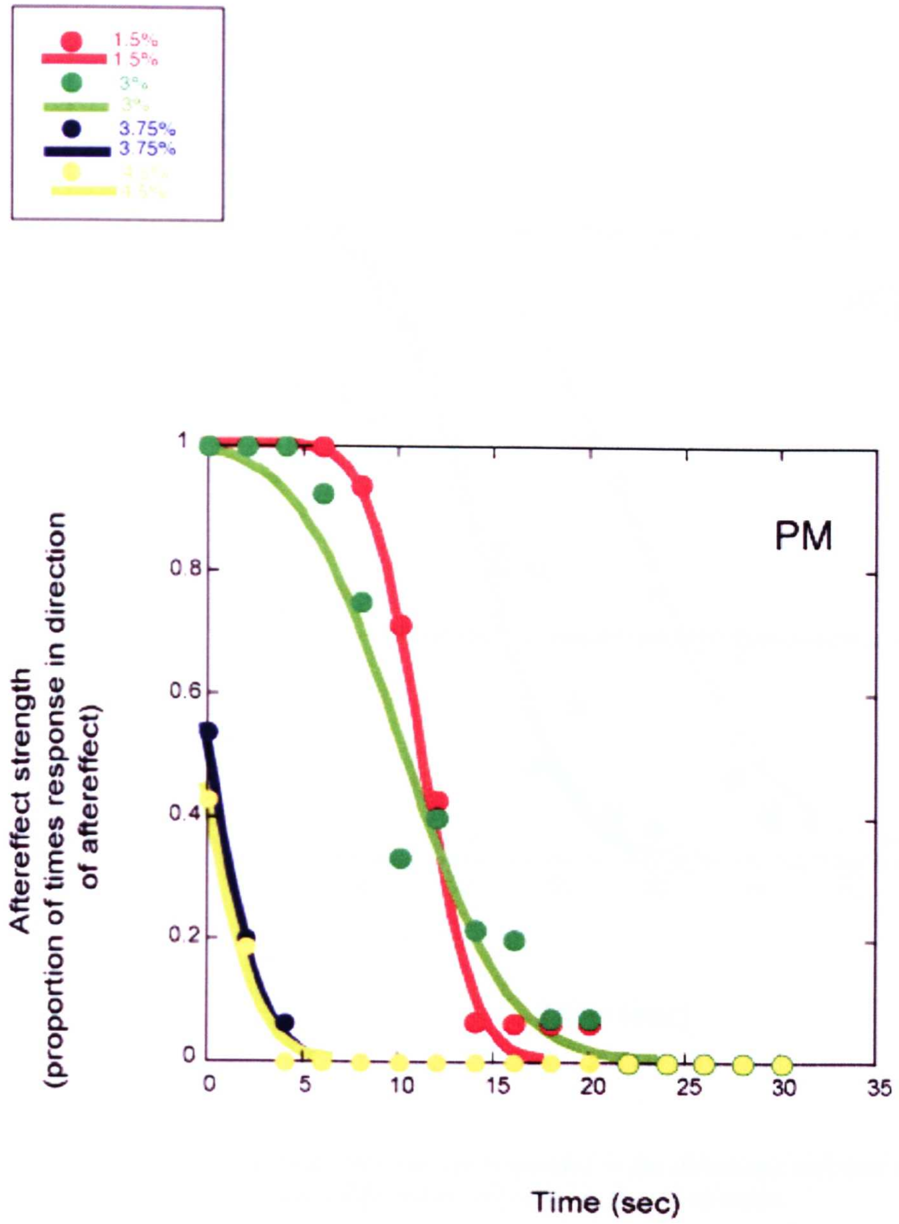


Fig 3 (v). *Proportion of times the observer responded in the direction consistent with a motion after-effect. Each curve represents a different velocity used in the test stimulus.*

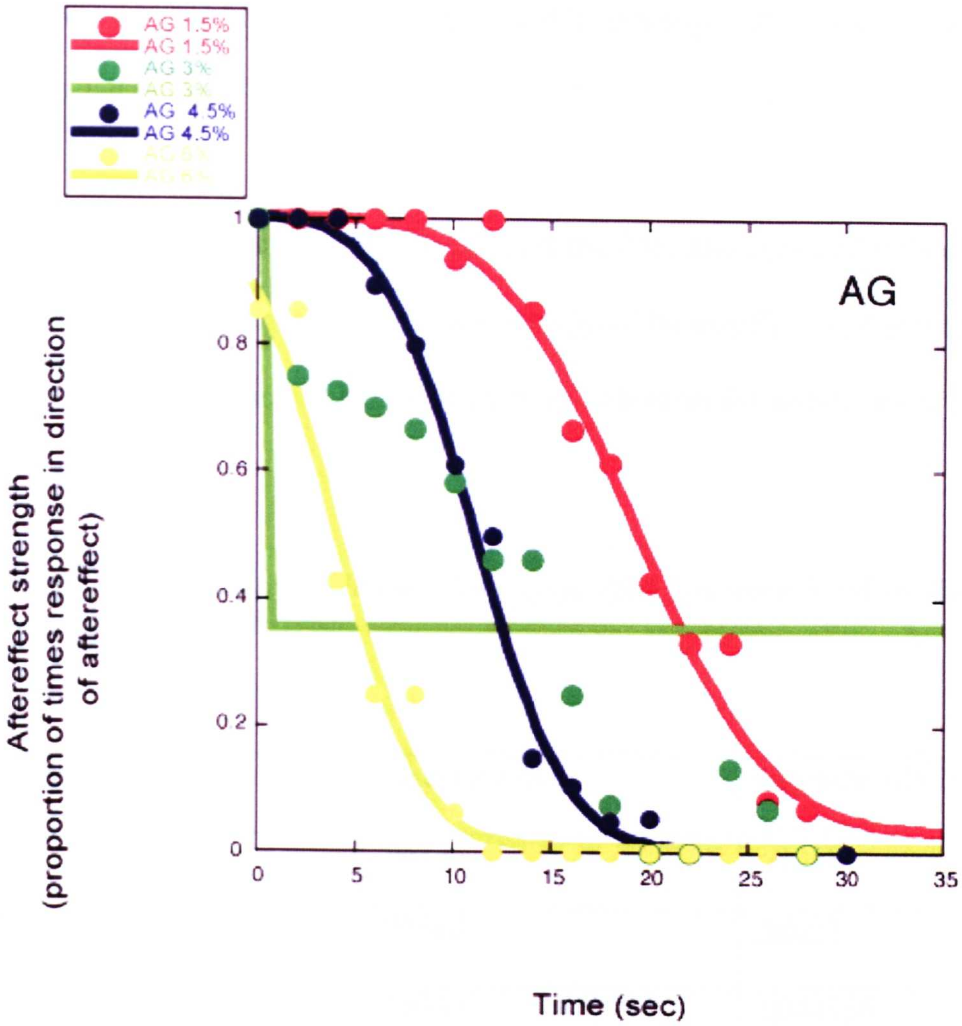


Fig 3 (vi). *Proportion of times the observer responded in the direction consistent with a motion after-effect. Each curve represents a different velocity used in the test stimulus.*

As test speed increased, response in the direction of the after-effect decreased. The PSE from the curves in these data was then used in a linear regression analysis. This gave an estimate of the relationship between test velocity and time to reach PSE. From this, an estimate for the strength of the test required to measure the after-effect is given at time zero. This is illustrated for each participant in Figure 4(i-vi). The closest results in terms of a linear fit are illustrated on a larger scale first to give the clearest example of the application of this technique. Following this results are presented for other participants.

An exponential function was also fitted to the PSE data obtained for each observer. The linear and exponential functions, in terms of the coefficient of determination, R^2 was determined. The value obtained for each observer for both types of fit are listed in Table 1.

Table 1. Comparison of linear and exponential functions fitted to the PSE data obtained for each observer.

Observer	Linear Fit (R^2)	Exponential Fit (R^2)
DS	.9613	.91368
PM	.77546	.38031
CA	.30367	.0044166
GO	.93319	.56505
AG	.87632	.88803
LO	.86444	.79547

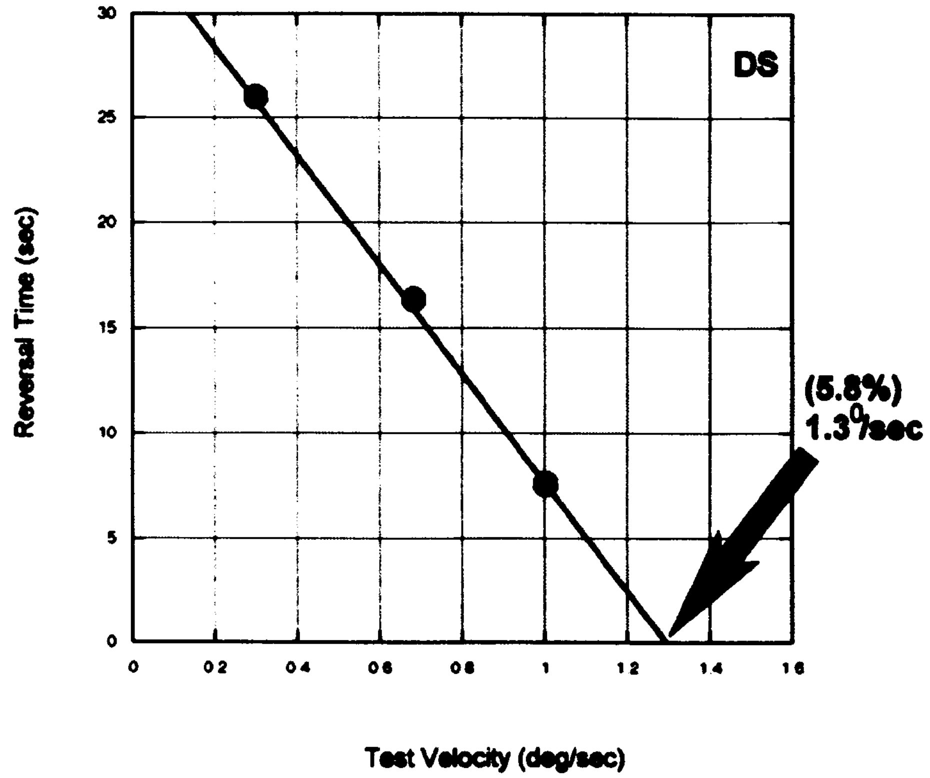


Fig.4 (i). *PSE plotted as a function of test velocity. Fitted with a linear regression to obtain an estimate of the magnitude of the after-effect at time zero. Estimate of this strength given in terms of percentage of adaptation speed (number in brackets) and in terms of real speed (deg/sec).*

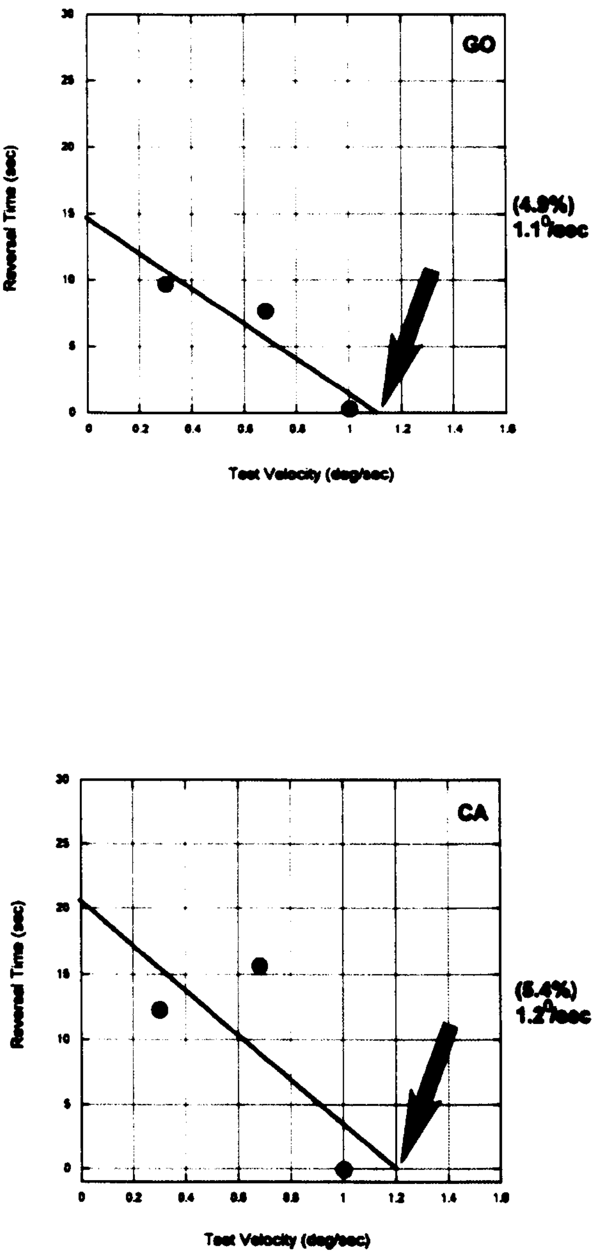
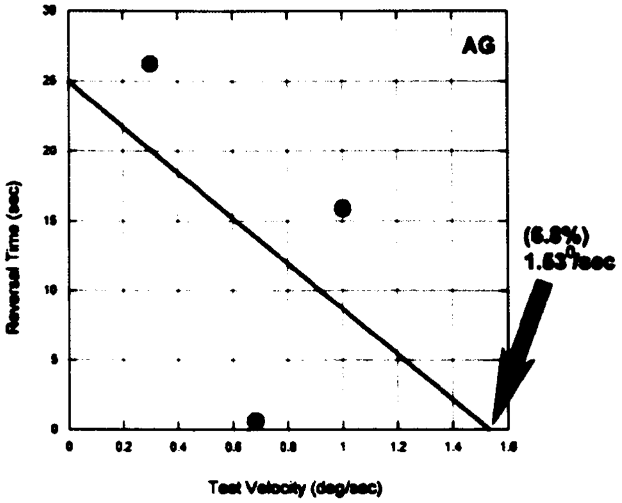
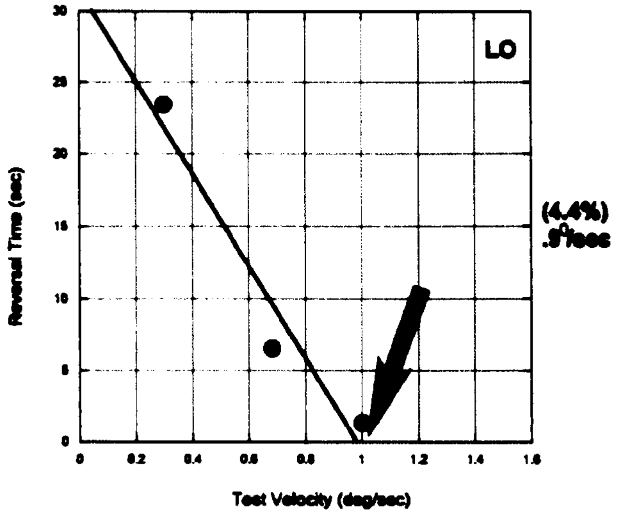


Fig.4 (ii & iii). *PSE plotted as a function of test velocity. Fitted with a linear regression to obtain an estimate of the magnitude of the after-effect at time zero. Estimate of this strength given in terms of percentage of adaptation speed (number in brackets) and in terms of real speed.*



(6.8%)
1.53°/sec



(4.4%)
.9°/sec

Fig.4 (iv & v). *PSE plotted as a function of test velocity. Fitted with a linear regression to obtain an estimate of the magnitude of the after-effect at time zero. Estimate of this strength given in terms of percentage of adaptation speed (number in brackets) and in terms of real speed.*

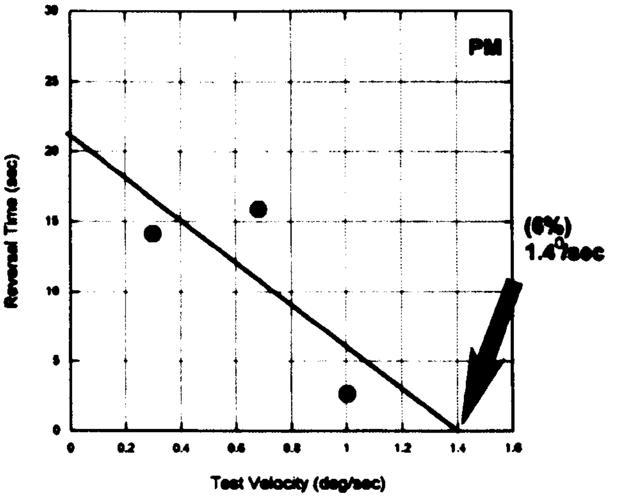


Fig.4(iv). *PSE plotted as a function of test velocity. Fitted with a linear regression to obtain an estimate of the magnitude of the after-effect at time zero. Estimate of this strength given in terms of percentage of adaptation speed (number in brackets) and in terms of real speed.*

A 15X3 ANOVA was done on the combined data revealing a main effect of the test, a main effect of the time and a significant interaction. Analysis of the main effects revealed two significant main effects of test (df= 1.7, 8.7, F=20.6, p,.001* corrected for sphericity) and time (df= 1.9,9.6, F=54.1 p<.000) and a significant interaction of test and time (df=2.1,10.8 F=4.3, p<.041). The combined data for this experiment are illustrated in Fig. 5 (i, & ii,)

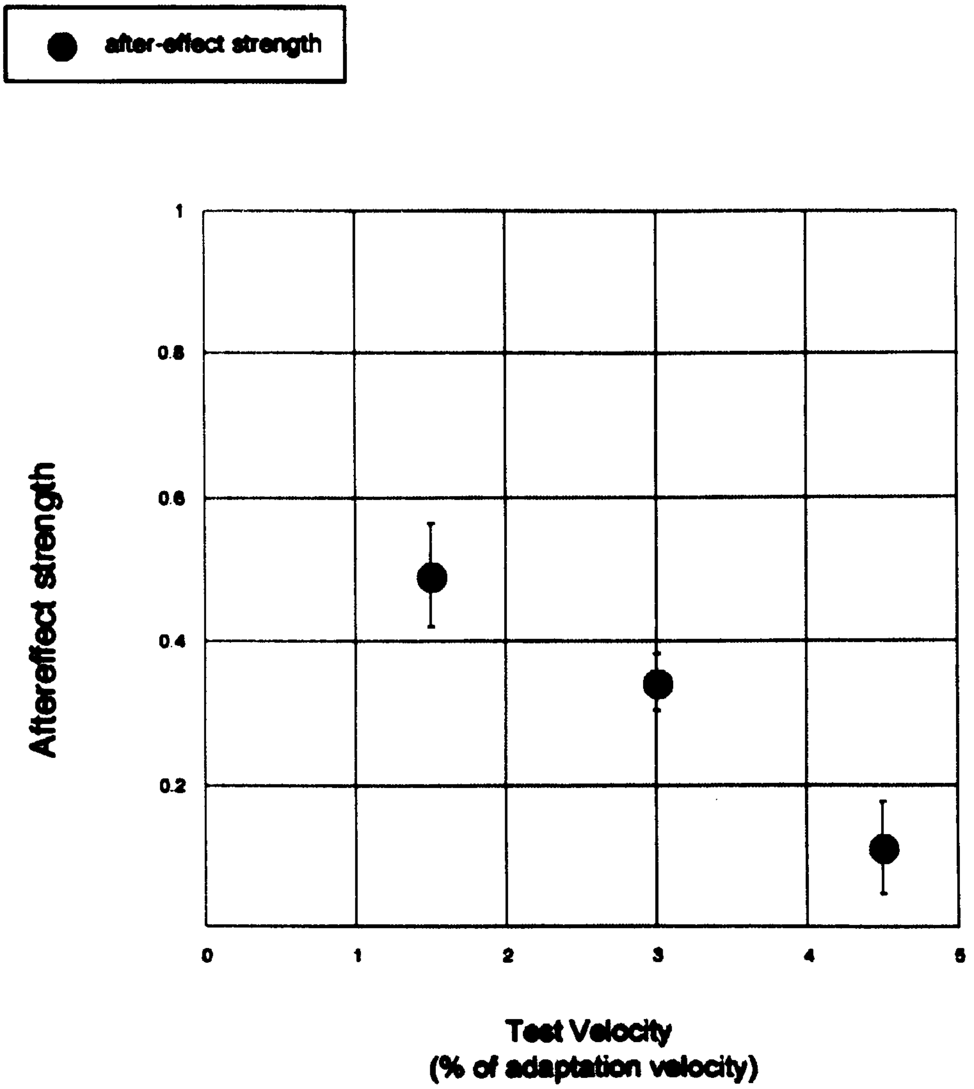


Fig. 5 *combined data: (i) variation in mean after-effect strength across test.*

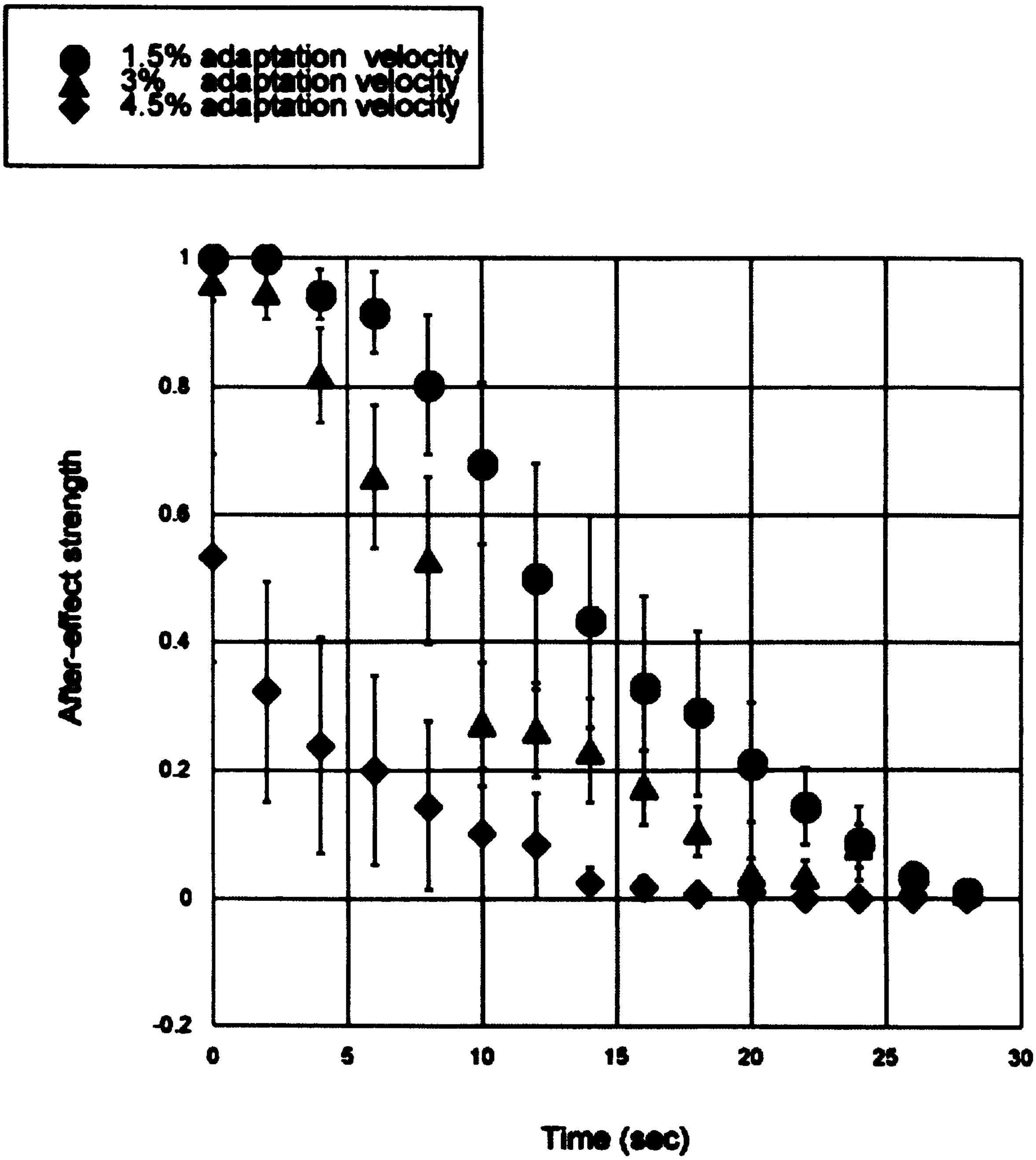


Fig 5 *combined data: (ii) variation in after-effect strength at each time and test velocity.*

Further analysis revealed simple main effects all occurring within the first seven time intervals. This highlighted a difference between the slowest velocity used and the fastest, however at time 5 and 6 there was also a significant difference between the medium and fastest velocity used.

Time	Difference	Significance
2	V1 vs V3	p< .033
3	V1 vs V3	p<.019
4	V1 vs V3	p<.011
5	V1 vs V2	p<.047
5	V1 vs V3	p<.013
6	V1 vs V2	p<.020
6	V1 vs V3	P<.017

Table 2: Table to show pairwise comparisons of test and time. Results show correction for Bonferonni multiple comparisons. V1=slow test, V2=medium test and V3=fast test.

The testing velocity had an effect on the perception of the after-effect. The lowest velocity used differed from both the medium and the fast and this occurred during the first 12 seconds of the experiment. The effect of test velocity appeared to be differential during the first 12 seconds of the experiment.

Specifically, the slowest velocity test used is different from the fastest velocity test used at time 2,3,4,5 and 6. The slowest velocity test used is also different from the medium velocity test used at time 5 and 6.

5.3 Discussion

In this experiment we generated a longer lasting after-effect and measured the persistence of the effect over time. This enabled an estimate of the after-effect strength at time zero for each participant (as shown for individual observers in Fig 3). Despite individual differences in the data obtained, the technique can be used as a measure of after-effect magnitude and duration.

Duration

As in the previous chapter, the after-effect duration decreased with increasing test velocity. Indeed, in this experiment the dependence of duration on test velocity was much more obvious. This is particularly clear in the case of observer DS (see Fig 4). The static after-effect was not explicitly tested in this experiment, because the static test stimulus would have been too salient to observers as positionally invariant. Furthermore, in the previous chapter it was demonstrated that the dynamics of the static after-effect were qualitatively different anyway.

The durations of the after-effects were longer than those measured in Chapter 4. This was partly due to the stimulus modifications, in particular using a longer adaptation time and presenting at a larger eccentricity. Consequently, measurement of the temporal dynamics of the after-effect was made much easier.

Magnitude

Again, as in chapter 3, the after-effect magnitude was estimated in two ways. In the first, the linear relationship between PSE and test velocity was exploited (see Figure 4) to calculate the after-effect strength at time zero. Of the three implementations of this measurement technique illustrated in this thesis, these data are by far the most consistent, with all participants demonstrated a time-zero strength of approximately 1 deg/sec (4.4 %). Mean value =1.2 deg/sec (5.3%) SD = .2 (.9%).

The second technique for measuring the after-effect magnitude is illustrated in Fig. 5(i). The total number of responses in the direction of the after-effect within the 30-sec test interval are plotted and averaged across the 5 participants. This graph illustrates that, as with the duration, the strength decreases with increasing test velocity, but also allows the instantaneous strength to be calculated by extrapolation. The figure of 5(ii) agrees well with the estimate obtained from the technique applied here. Obviously, with three points on each of these graphs, it cannot be argued that a linear relationship between either strength or PSE and test velocity has been definitively demonstrated. However, in the absence of a theoretical prediction from the literature, an assumption of linearity seems to be a reasonable first approximation. It is hoped that future experiments will explore the precise nature of these dependences.

Implications of the results

Current models of the motion after-effect (eg. Mather & Harris, 1998; Mather 1980; Sutherland, 1961) indicate that the perception of the reversal of motion is due to the unbalanced activity of populations of neurons tuned to a preferred direction. This is supported physiologically by direction-specific neurones being found in macaque MT (van Wezel & Britten, 2001).

Work on the motion after-effect has led to the suggestion that there are two temporally tuned channels in the visual system, one responsible for high speed motion and the other for low speed motion. It has even been proposed that there are multiple adaptation sites in the brain when adapting to motion (Pantle, 1998).

These results seem to be at odds with these models and ideas. One potential problem is that the test stimulus, when presented at high speeds, contained so much motion energy that it suppressed the perception of any after-effects, whereas the lower-speed test stimuli only gently stimulate the adapted mechanism and consequently show a more salient after-effect. It might be argued that presenting a test stimulus at lower contrasts would be beneficial in this respect. However, the relationship between MAE perception and contrast is not straightforward (Nishida, et al 1997a), so the results would not necessarily be straightforward to interpret.

It is possible that in this experiment high-speed channels normally involved in the dynamic MAE were not stimulated and instead there was a resultant residual static MAE which was picked up by our slow-moving test stimuli.

However, as they stand, the results would appear to question the separation between high- and low-speed mechanisms, at least when it comes to the motion after-effect. Speed tuning of neurons has been shown to cluster at least in area MT (Liu & Newsome, 2003). Consequently, this perception of the reversal of motion indicates that there may be interactions between spatially separate populations of speed-tuned neurons.

Ledgeway & Smith, (1997) report similar principles involved in velocity coding across motion type (using first and second order motion). It may also be that there are similarities between high and low speed adaptation processes, but not necessarily originating from the same mechanism.

The present study does not necessarily point towards differential adaptation sites according to the velocity of motion. Instead this study supports relations between high speed and low speed units occurring during adaptation. A possible interpretation is that during the testing carried out in the low speed range this has stimulated an overlapping region between high speed tuned and low speed tuned units.

5.4 Summary

Here we present a robust method for capturing the full temporal dynamics of the motion after-effect. This includes an estimate of the strength at time zero, and also how the magnitude of the effect is varying with time.

Furthermore, we applied the use of a high speed adaptation stimulus and a slow speed test. It is a currently debated area as to whether multiple or single sites are involved in motion processing, and what the relationship of these sites is to speed encoding. This experiment indicated that even when using a high speed adaptation stimuli, the perception of direction can be altered using a slow speed test. This may indicate a common site of adaptation processing in motion processing, even at different speeds.

Chapter 6: Perception of motion transparency after depth contingent motion after-effect

In the previous work shown we have looked at the temporal dynamics of adaptation to the cues of motion and disparity. As there is evidence for simultaneity of processing of both motion and disparity, it is useful to examine the interaction of the two cues. Despite being researched, the relationship of the cues is still unresolved. The next experiment looks at a combination of adaptation to motion and disparity, employing a contingent after-effect experiment. We look specifically at the effects of this adaptation on the perception of a temporally ambiguous stimulus, that gives a perception of motion transparency. We find that adaptation to non-transparent motion presented at a particular binocular disparity can bias the depth order judgement of surfaces. This bias was consistent with a depth contingent MAE. Previous work has demonstrated the MAE is contingent on depth (Verstraten, 1994), and MAE direction is dependent on surface order during adaptation (Sohn & Sieffert, 2006). We extend current findings by demonstrating the influence of adaptation to non-transparent motion and disparity also can influence the perception of transparent stimuli. We find that participant perception of ambiguous stimuli was influenced by adaptation contingent with the predicted after-effect, despite the lack of adaptation to a transparent surface. This again highlights the importance of neural structures tuned to both disparity and direction.

6.1 Overview

In the experiments previously reported, the focus has been on the response of the visual system to a change to either depth or motion (the DAE and MAE). Observers have been exposed to one particular stimulus attribute (disparity or velocity) and have been tested with varying degrees of that stimulus attribute. Consequently, the results could reflect the observer's perception of that aspect of the stimuli alone, which could be argued to originate from simple low level processing. However, as has been a topic of debate (Howard & Rogers, 2002), there are most likely multiple sites of adaptation involved when processing incoming visual information (Mather, 1980). Evidence for this has been demonstrated at least in the processing of the motion after-effect (Nishida, 1995). Furthermore, the close inter-relationship of motion and binocular processing has been of increasing importance for models of motion processing and overall sensory processing in the environment (Mather, 1998). It is therefore important to address the interrelationship between potentially tied adaptive mechanisms, with a view to tackling the issue of related processing mechanisms.

There is also the possibility that common associative processes reflect a higher degree of processing (although motion and depth processing cells appear at early and late stages of the visual processing pathway, see Hubel & Wiesel, 1962). The next experiment seeks to look at the relationship between adaptation between motion and depth. One method of assessing this is by employing a contingent after-effect paradigm (see Section1.2 below).

These experiments have been useful in the investigation of associative processing because they give clues as to (i) multiple versus single sites of processing, and (ii) level of processing (low versus high in the visual processing hierarchy) and (iii) similarity of adaptation mechanisms. This chapter will first outline the usefulness of the contingent after-effect paradigm, and then present a study looking at the associative processing between depth and motion processing.

6.2 Techniques and Theoretical Importance of Contingent Adaptation After-effects (CAA)

A technique that can be utilised to address the nature of such after-effects has been developed through the use of Contingent Adaptation After-effect (CAA) experiments (Haijiang, 2006). These experiments address after-effects that develop through exposure to associated events in the environment. This can also be viewed as a type of learning. This has similarities to the concept of association, which has been important in Psychology since the introduction of experiments on classical conditioning, and is implicated in theories addressing the nature of learning and conditioned behaviour (Gleitman, 1998). Understanding the nature of how the system responds to associative information is of critical importance as many models of information processing are directly linked to assessing the incoming statistics of the natural environment (e.g Wainright, 1999). This means that if the goal of visual processing is the efficient transmission of incoming information, then this information must be interpreted from the incoming light signals from the environment. It has been demonstrated that this information can be represented in a statistical way, when information in the environment is represented this way, some observers' biases in human perception can be accounted for (e.g see Howe & Purves, 2002).

The analysis of environmental contingencies are of theoretical importance to such models, and the study of contingent after-effects may be the first step in disentangling the underlying mechanisms responsible for detecting novel correlations in the environment (Barlow, 1990).

The experimental paradigm of using contingent adaptation after-effects is concerned with the association between stimulus domains. It has been used in the field of visual perception mainly to try to address the level at which adaptation is occurring, through studying the nature of contingent after-effects. This approach has two main advantages over uni-dimensional adaptation in that (i) contingency paradigms indicate level of processing at the associative level and help distinguish level of operation of mechanisms in theories of after-effects and (ii) can be argued to tackle a more ecologically valid relationship to the natural environment- we are rarely presented with situations with one sense input alone. This chapter presents an experiment designed to investigate the relationship between depth and motion processing in the visual system.

6.3 History of Contingent After-effect Experiments

In the contingent after-effect paradigm, there is an adaptation to an association present in the stimulus. The McCollough effect (1965) is not only the first but potentially the most famous demonstration of a contingent after-effect. Following adaptation to coloured gratings of different orientations, there is a colour after-effect contingent on subsequent gratings orientation. Research on the underlying mechanisms of this effect continue, with one theory being that it is the joint coding of orientation and colour that generate the effect (McCollough, 1965). Another theory is that it could be fatigue of cells underlying the effect, but this does not explain the association between the orientation and the colour. This highlights the importance of the interaction of modalities in the visual system.

A further interesting contingent after-effect is revealed by examining the relationship between texture and density (Durgin, 1996). In this study it was reported that visual texture density is quite malleable and can be made to be contingent on the colour of the surrounding frame, a related finding to the McCollogh effect. It is interesting to point out here that with certain stimulus combinations, such as colour and motion, it is harder to elicit a contingent after-effect. The contingency of density and texture colour perhaps points to the similarity of coding of these cues. Indeed the resistance of some associations to adaptation was reported in early experiments by Stratton (1897), where prism experiments led to the inversion of some objects in the visual field following adaptation whereas some objects remained veridically perceived. This is an interesting point about adaptation experiments, in that the effects appear to be specific to certain associations, potentially highlighting the specific aspects of the nature of the coding of visual stimuli.

Indeed, further exploration utilising the contingent after-effect paradigm illustrates the importance of associative processing in perception. This has generated many other studies, explicitly examining cortical plasticity between areas, such as vision and audition. Recanzone (1998) demonstrated the phenomena labelled the 'Ventriloquism after-effect'. This effect occurs when human participants are exposed to spatially disparate and simultaneously presented acoustic and visual stimuli. This leads to changes in auditory space perception, such that participants following adaptation mislocalize the source of sound in a manner contingent on adaptation. This is an interesting demonstration that is suggested to reflect changes in cortical representation between modalities, perhaps indicating the overall malleability of sensory processing.

These illustrations (the McCollough Effect (McCollough (1965))), texture-colour density after-effect (Durgin (1996)), and the Ventriloquism after-effect (Recanzone, 1998) all demonstrate that not only is adaptation to associations possible even across senses, but that a strong measurable after-effect is produced following adaptation. The time scale of these effects appears to vary, with the McCollough being the longest (lasting up to 24 hours, Jones & Holding, 1975) and other effects – for example the Ventriloquism After-effect- last approximately proportional to the time of exposure during adaptation (Recanzone, 1998).

6.4 Theoretical Summary

Theoretically, these studies are important. Early theories (Sutherland, 1961; Barlow & Hill, 1963; Mather; 1980, Harris, 1981) give account of adaptation in terms of neural fatigue and do not ascribe functional significance to the phenomena. More recent theories of sensory processing are focussing on the statistical information represented in the visual system. Exploration into contingent after-effects may provide insight into the nature of visual coding (Barlow, 1990).

In terms of sensory coding hypothesis, Barlow (1990) argued that these effects could underlie the nature of sensory space by highlighting the search for novel associations in the environment. He proposes a 'principle of repulsion' to explain the change in sensory space that occurs when a novel pairing (such as orientation and colour) appears in the environment. The advantage of this approach is that it allows for the possibility of representing the contingencies of an area that could be distinguished by a sensory system, and is plausible on a physiological level.

Other theories of sensory coding explain a functional significance of adaptation in terms of coding of population of neurons, and posit gain control as a means of explaining after-effects. An argument in favour of a functional benefit of adaptation comes from increased sensitivity that can be observed and measured during adaptation (e.g Clifford & Langley, 1996). If adaptation is viewed in terms of recalibration of the visual system to the world, this could potentially be explored through the use of a contingent after-effect paradigm.

6.5 Motion and Depth Processing

The relationship between motion and depth processing provides a current issue of research (see Mather, 1998). There is evidence to suggest combined processing of motion and depth, and this is particularly supported by neurons MT being specifically tuned to motion and disparity (Bradley et al, 1995). Bradley et al (1995) examine the role of disparity in MT in macaques. They demonstrate that inhibition in MT affects motion signals that are also similar in the terms of disparity. This suggests that different depths can be possibly represented at the level of MT.

This physiological finding also makes sense from a theoretical point of view, given that processing of motion and depth could be quite similar from a computational perspective of sensory processing, requiring the differentiation of two differing images (one in space and the other in time).

Anstis & Harris (1974) looked at depth contingent motion after-effects, and also vice versa. They utilised random dots on discs placed at different depths, and observed rotation at different depth locations. It was reported that there was a motion after-effect contingent on depth adaptation, and also a depth after-effect contingent on motion adaptation. The magnitude of the after-effect was in the scale of minutes[4], but this study highlighted the adaptation contingency between these two modalities, and has contributed to the theoretical idea of a common processing pathway for motion and depth processing.

Furthermore, it has been demonstrated that there can be a reversal of motion in depth, which is contingent on disparity (Smith, 1976). Further studies looking at adaptation to gratings in a moving depth plane and then testing with static on the same and different depth planes also illustrate a MAE contingent upon depth (Lehmkuhle & Fox (1977), Fox, (1982) cited in Mather et al, 1998).

Later studies have focused on the relationship between bi-vectorial motion and direction of motion in the perception of an after-effect (Verstraten, et al (1994)). An interesting finding here is that the MAE direction, even for transparent motion, is not contingent on the direction of the planes used during adaptation, but on the combined direction of the planes adapted too. It has also been shown that there is a motion after-effect contingent on the depth of the adaptation stimulus, with (similar to other effects) it being highlighted that the degree of similarity between adaptation and test is crucial of the generation of an after-effect. This demonstrates cells which respond selectively to a particular direction of motion at a given binocular disparity.

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[4] By the scale of minutes this means that following a period of adaptation, the range of after-effect period changed over recording times of minutes. This can be contrasted with after-effects that last a few seconds (e.g for MAE Kanai et al, 2005) or over a day (e.g orientation & colour, Jones et al, 1975)

6.6 Present Experiment Rationale & Theoretical Predictions

The present study demonstrates a depth contingent motion after-effect applied to an ambiguous stimulus, that of motion transparency. It has been demonstrated that there is a depth contingent motion after-effect (e.g Anstis & Harris; 1974) that is strongest when adaptation and test are close in disparity. It has also been recently demonstrated that training can be used to influence observer's conscious perception of the world, utilising ambiguous stimuli and training with cues (Haijiang, 2006). In this experiment, we seek to address if the setup of a contingent after-effect can influence participants experience of transparent motion. During this experiment, motion was paired with disparity. This was carried out in two planes of depth, in the top and bottom regions of the screen. During the experiment, direction of motion was also paired with a particular disparity, either in front or behind of fixation. This differs from other studies in that participants were not adapted (or trained) on the test stimulus, but faced a different stimuli on the test trials from that which was adapted too. Previous studies have utilised the same stimuli during adaptation and test, which has the advantage of giving a high degree of transfer of after-effects (degree of similarity between adaptation and test being one of the main predictors or after-effect magnitude and duration (Pantle, 1998)) however, the setup of a bias in the testing phase of a novel stimuli would lend strength to the prior role of experience governing perception in the world. Transparent motion is an ideal testing stimuli because of the elements of the adaptation pairing, but also in that it provides a bi-stable stimulus within the context of the experiment. The independent variable in this experiment is the pairing of motion and depth in the adaptation phase of the experiment. During this point participants will experience the movement of a RDK at a particular plane of depth. This should provide a disparity cue and a motion cue. Following previous work, this should elicit a tangible motion after-effect and a tangible depth after-effect. Following the generation of these effects, the observer's perception of motion transparency following adaptation will be tested. Given theories that adaptation can govern perception, and that this can be carried out during relatively short time frames, it is predicted that the presence of adaptation will have an effect on the perception of transparent motion. Specifically, the hypothesis of the experiment is that following adaptation to motion in depth, observers' perception of transparent stimuli will be biased in a manner contingent with a motion after-effect. This will be expressed as an effect on the dependent variable, which will be the number of trials the observer perceives the MAE consistent surface in front of the other surface. This is expressed as the proportion of times the observer responds in the way that indicates that perception is being mediated by the adaptation pairing. This is an interesting experiment as it is unclear how the after-effect will interact with the stimuli. As similarity of adapting and test stimuli is critical in the generation of an after-effect, it is possible that there would be no effect as the transparent stimuli although similar in base components, will also be at a different horizontal disparity. The null hypothesis is therefore that there will be no influence of the pairing during the adaptation phase on observers' perception of the transparent surface, expressed as the ratio of times observers perceive the transparent surface in a manner consistent with an after-effect contingent on the motion and depth present in the adaptation.

To summarize the conditions of this experiment, we predict that if there is a depth contingent motion after-effect which can modify the previously established bias for transparent surfaces (Mamassian & Wallace, 2003), then this should be expressed as a change in the perceived depth order of a transparent surface following adaptation. In this experiment the adaptation consists of exposing the observer to a specific pairing of motion and disparity. The null hypothesis is therefore that following adaptation there will be no change in the depth perception of transparent motion. The alternative hypothesis is that the observer's perception of transparent motion is contingent upon the pairing of disparity and direction of motion present during the adaptation period. The exact predictions of this experiment are outlined in Table 1.

Table 1. Table to show predictions of experiment.

Depth Contingent Motion After Effect	PRESENT	ABSENT
Expected effect on observer's bias	Increase in proportion of responses post adaptation in direction *consistent with motion after-effect contingent on depth*	No increase in proportion of responses post adaptation in direction *consistent with motion after-effect contingent on depth*

6.7 Rationale, Procedure & Design

The experiment follows the common pre-test, adaptation, post-test setup often employed in adaptation experiments. First, participants were tested on a perceptually bi-stable stimulus, and asked to make a judgment about the depth of this stimulus. During the adaptation phase, they were exposed to a pairing of motion and depth. Following this, they were again presented with an identical test that they were subject to in the pre-test session. It is predicted that if there is a depth contingent motion after-effect this should be expressed a difference post-test of the transparent surface. Due to the specific pairing between one direction of motion and one depth this should lead to a specific pairing of direction of motion and depth following adaptation.

Stimuli

Random Dot Kinematograms (RDK) were generated for the experiment using the Psychophysics Toolbox and MATLAB (Brainard, 1997; Pelli, 1997). These were viewed through a standard Wheatstone stereoscope setup. The computer used was a Sony Trinitron 21 inch monitor. Viewing distance was 214 cm. Participants were presented with two planes of moving dots, placed concurrently, such that a transparent surface with no depth was generated (Testing phase, see Fig 1).

Test phase was identical for pre and post testing. Fig 1 depicts the two possible locations of the test phase, however in the experiment these tests were identical. Two planes of dots, identical in generation but moving in opposite directions, were superimposed. This led to the perception of a transparent motion surface, consisting of two surfaces (one moving to the left and one moving to the right). This is predicted to be a perceptually bi-stable phenomenon, as due to the lack of depth separation in the stimulus, interpretation of either surface 'in front' is likely. It has already been demonstrated that perceptual cues can be used to bias which surface appears in front (Mamassian & Wallace, 03). These perceptual cues are the polarity of the surface (black or white) and the orientation. However, in this setup, there is nothing present to bias the system, leaving it a bi-stable and therefore ambiguous stimulus. No top up was used in between test trial.

This phase was used during testing pre-adaptation and testing post-adaptation. There was no depth present between the two planes of dots, as they only differed in their direction of motion. Direction of motion was lateral in order to control for eye movements, with one plane of dots moving right and one plane of dots moving left. There was a brief presentation time, where participants were asked to make a decision as to what surface was in front (approx .2sec). This formed a 2AFC setup and 240 (blocked) trials were run per participant. There were 48 trials in one run, then adaptation for a minute, then 48 trials for the testing period. This was then carried out 5 times to give the total of 240 trials that is depicted in Fig 2 (Graph to show pre & post bias for perception of depth of transparent surface). No top up procedure was used.

During the adaptation phase, observers were not required to respond in any way. They were instructed in the Wheatstone stereoscope setup, to fixate as much as possible on the centre of the screen. During this time, they were presented with two identical RDK's of motion, either in the lower or upper field of the screen. These differed in their direction of motion and in plane of depth. This is illustrated in Fig. 1.

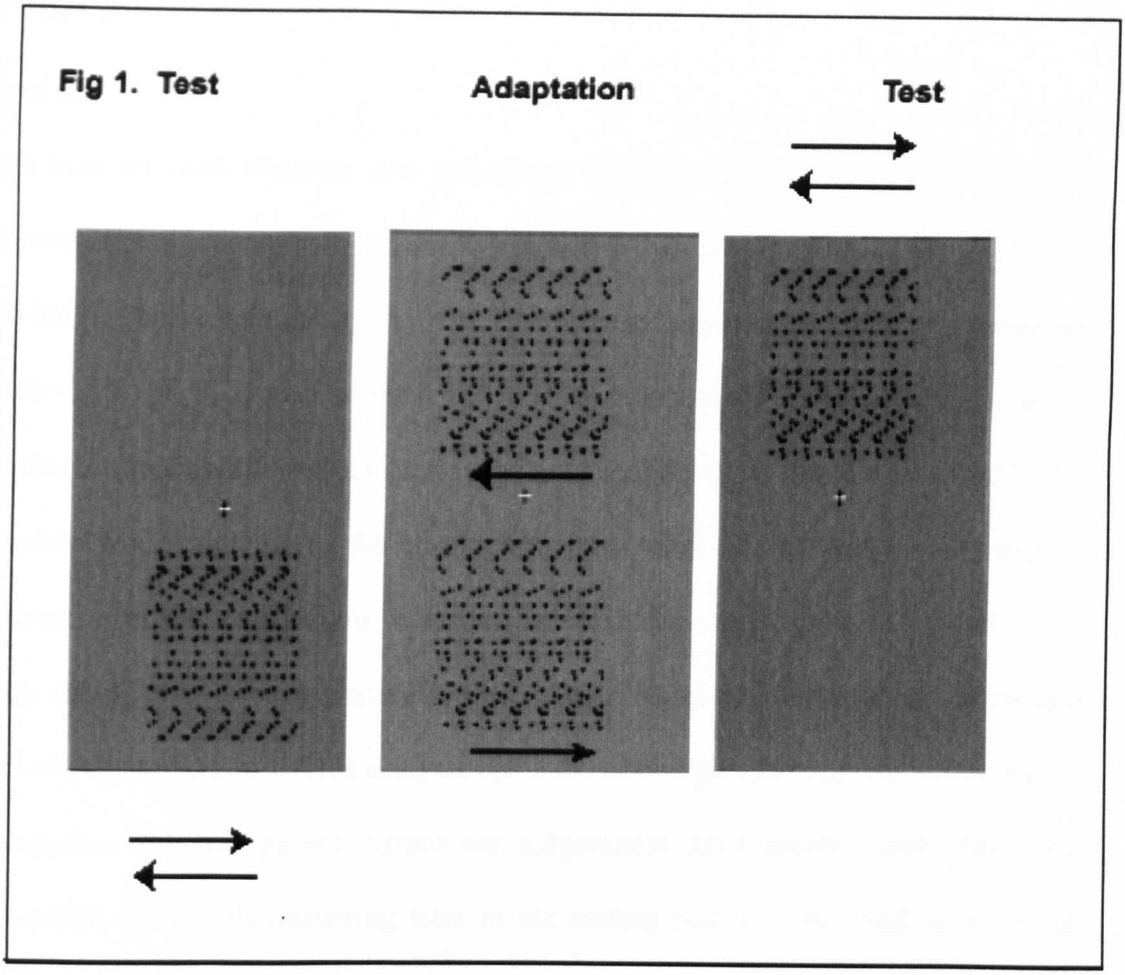

Fig 1. Stimuli throughout experiment. Two planes of dots alternated from lower to upper half of the screen, moving in opposite directions and placed either in front or behind of fixation. To prevent eye movements two such movies were presented out of phase (but never simultaneously) above and below fixation.

6.8 Participants

Seven participants participated in the experiment, including the author (LO). All had normal or corrected to normal vision. All, excluding the author, were naïve to the purpose of the experiment. All were debriefed following the experiment.

6.9 Results

Analysis

The bias for each observer was calculated from the proportion of responses for motion direction perceived in front. Observer's biases for which direction of motion moved in front were significantly different between pre and post adaptation sessions (t(6)=2.81, p<.031, two tailed), in a manner mostly consistent with a depth contingent motion after-effect. Results of the experiment are illustrated in Fig 2. We checked for dissipation of the contingent after-effect due to the lack of a top-up procedure in this experiment, meaning that the after-effect obtained in early test trials should be greater than that obtained in later test trials. This was carried out and included in Appendix 1. This analysis did show a stronger effect of adaptation on the perception of a transparent surface for judgements made shortly after adaptation compared with trials occurring later in the testing period. This finding serves to support that an observer's bias for the perception of a transparent surface can be modified by adaptation to motion and disparity, and this effect is greatest following adaptation. Indeed, the fact that we find an effect without the implementation of a topping up procedure indicated the robustness of the effect for changing an observers bias for the perception of a transparent surface.

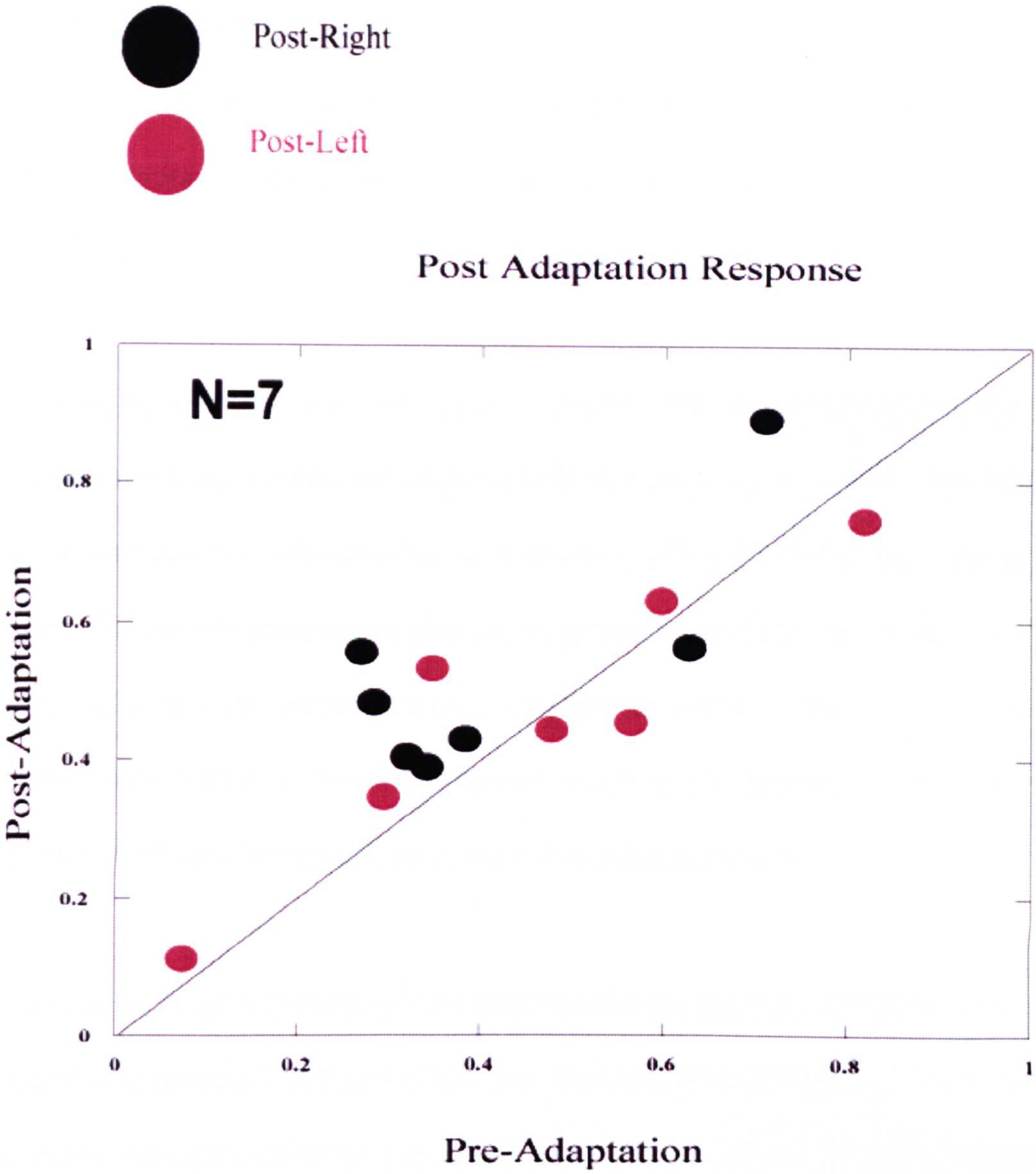

Fig 2. Pre and Post Adaptation Bias. Anything to the left of the diagonal line indicates a bias consistent with that predicted from adaptation to a pairing of motion direction and disparity viewed during adaptation.

6.10 Motion and Disparity Processing

We demonstrate that the perception of motion transparency can be biased by motion and depth adaptation. Specifically, the bias is in a manner consistent with a depth contingent MAE.

Previous work has shown that the similarity in disparity between adaptation and test is critical in generating a depth contingent MAE (Verstraten et al, 1994). This has been used to indicate the local structure of disparity and motion processing systems in the brain. Our results demonstrate that the adaptation to disparity and motion can be used to influence the perception of a transparent surface. This surface was presented at zero disparity. In an ambiguous situation the disparity and motion information can be used to bias the perception of transparent motion.

Recent results by Sohn & Sieffert (2006) demonstrate that motion information may be represented in terms of surface depth order. In a similar paradigm they reported that the depth contingent MAE was perceived in a direction opposite to the surface that was in front during the adaptation phase (using transparent stimuli). In this experiment we did not find a bias for which surface was presented in front over the adaptation phase. When adapting to non-transparent stimuli, we report that the depth seen in a transparent surface is opposite to adaptation plane and direction.

6.11 Theoretical Conclusion

The earliest theory of adaptation is the fatigue model. With the current findings, the fact that adaptation to motion at a particular depth plane could influence the subsequent perception of an ambiguous stimulus suggests that there are higher-level processes ongoing.

More recent theories have looked at adaptation in terms of perceptual learning (Haijiang et al, 2006). The results in this experiment could be due to a learning of the relationship between depth and motion, and adaptation to this being used as a new cue when interpreting an ambiguous stimulus.

6.12 Summary

This study has addressed adaptation in response to both motion and depth stimuli, in an ambiguous context (applied to motion transparency). This was a contingent after-effect experiment, which has strong links to learning associations between stimuli and the effect this has on novel stimuli. It was found that the relationship between motion and depth could be adapted to, in a way that influences perception of ambiguous new stimuli in a predictable manner. Of direct interest is the fact that the adaptation was very different from the test and did not have a similar binocular disparity. This suggests higher level cognitive processing in the perception of surface depth order from motion and disparity information.

Chapter 7: General Discussion

7.1 Introduction

This thesis has addressed a number of issues regarding the nature and measurement of visual after-effects. As has been described in Chapters 1 and 2, adaptation and after-effect phenomena have generated interest amongst philosophers and vision scientists for centuries. However, whilst the adaptation paradigm has been applied widely in research, a full theoretical explanation for this phenomenon has yet to be fully developed.

Initial theories focused on the fatigue of visual neurons, leading to terms like 'recovery period' and 'decay' of the after-effect (Clifford & Rhodes, 2005). This approach is now changing with the emergence of a more complex view of after-effects, characterising them as part of a dynamic system, capable of recalibrating itself dependent on environmental conditions.

With this change in theory more sophisticated measurements are required to obtain accurate insight into adaptation phenomena. This is especially true given the recent findings that the visual system can be trained over time to respond to contingencies in the environment (Haijiang et al, 2006). Temporal aspects of these associative processes may be important when aiming to model underlying mechanisms.

This thesis therefore began with an examination of after-effects. We were first interested in obtaining a measure of after-effects following adaptation. We did this in two different visual domains: depth and motion. We then moved on to investigate adaptation to motion and depth information when they were contingent upon each other.

In the next section we summarise the results from each chapter individually and draw conclusions regarding how our findings impact current research. Following this, general implications of this thesis are suggested and possible applications for future research are outlined. Finally, the general conclusions that may be drawn from the research are summarised.

7.2 Summary of Findings

In Chapter 3 we investigated the application of a technique for capturing the temporal dynamics of the depth after-effect. Participants adapted to a fronto-parallel surface displayed in front of a fixation point for 30 seconds. The surface viewed was depicted by binocular disparities of random dots refreshed every half-second. Vergence was maintained using a surrounding texture with zero disparity. Following a brief interval, a similar surface was presented for 30 seconds at a disparity chosen differently from trial to trial. During this test phase, participants were asked to judge the perceived depth (in front or behind) of the surface at the sound of a beep presented on average every 2 seconds. Repeating these sequences of adaptation and test phases allowed us to measure the dynamics of the after-effect for different test depths. We found that the dynamics of the after-effect depended on the disparity of the test surface. As predicted, the smaller the disparity of the test, the longer the after-effect lasted. The time constant of the after-effect was defined as the time needed to reach the point of subjective equality (where percepts are equally distributed in front and behind fixation). These time constants increased as the test disparity decreased, even beyond the critical disparity that produced a consistent initial after-effect.

We thus successfully demonstrated that this new technique for investigating the temporal dynamics of perceptual after-effects was both possible to perform and practically useful for the measurement of the depth after-effect. Unlike standard nulling techniques, our paradigm allowed us to measure the full temporal variation of the after-effect. In addition, our method is more objective than the traditional technique of estimating the duration of the after-effect.

In Chapter 4 we attempted to measure the movement after-effect using a similar technique. Specifically, we measured the temporal dynamics of movement after-effects when the test stimulus was presented at various speeds. Participants adapted to random dot kinematograms (RDKs) for a period of 8 seconds. To reduce eye movements, two RDKs were placed on either side of the fixation point, moving in opposite directions (e.g. outwards motion). Following a brief interval, the adapting stimuli were replaced by test stimuli whose direction was identical (e.g. outwards) but whose speed was a fraction of the adapting speed. For slow test speeds, the perceived direction of the test stimulus was initially opposite to its physical direction (e.g. inwards) and slowly reverted to the true direction (e.g. outwards). We prompted observers to repeatedly judge the perceived direction of the test stimulus in order to estimate the time of reversal. In this experiment we could not obtain Pse's for the data, however following fitting the data we took the tangent to the point of inflection as our measure of the duration of the movement after-effect, and estimated these durations for various test speeds. We found that the duration of the after-effect depended on the speed of the test surface. Specifically, the slower the speed of the test stimulus, the longer the after-effect lasted. This new method of investigating the after-effects thus successfully provided an estimate of the temporal dynamics of the movement after-effect. This experiment established the parameters for the data presented in Chapter 5.

In Chapter 5, we again were interested in measuring the temporal dynamics of the movement after-effect through application of a nulling technique. Participants adapted to two drifting Gabor patches (speed = 22.5 deg/sec) for a period of 48 seconds. To reduce eye movements, these were placed either side of the fixation point, moving in opposite directions (e.g. both moving outwards). Following a brief interval, test stimuli were presented which were identical to the adapting stimuli except for their speed. At slow test speeds, the perceived direction of the test stimulus was initially opposite to its physical direction (e.g. inwards) and slowly reverted to the true direction (e.g. outwards). We prompted observers to judge repeatedly the perceived direction of the test stimulus in order to estimate the time of reversal. Responses were sampled on average every two seconds for a total period of 30 seconds. The time of reversal was our measure of the duration of the movement after-effect, and estimated durations were measured for various test speeds. As predicted, observers' perceived direction of motion changed over the testing period, depending on the speed introduced into the test stimulus. From looking at the change in observers' responses over the testing period for different speeds, we derived an estimate of how the initial strength of the after-effect and its time constant changed as a function of test speed, giving a clearer picture of the temporal dynamics of this MAE.

In Chapter 6 we moved on to investigate contingent after-effects. Transparent motion can result in bistable percepts because of an ambiguity about which surface is in front and which one is behind. Previous work has shown that observers have an idiosyncratic bias for perceiving one particular direction of motion in front (Mamassian & Wallace, 2003) and that segregation cues, such as contrast, can influence the temporal dynamics of the alternation of which surface is perceived in front (McArthur & Mamassian, 2005). Here, we looked at the effect of adaptation to motion in depth (Anstis & Harris, 1974) on an observer's bias for transparent motion. On both pre- and post-adaptation sessions, observers were presented with brief random–dot kinematograms (RDKs) where two transparent planes were displayed in the zero-disparity plane. Their task was to report the direction of motion of the plane perceived in front. In the adaptation period, observers were presented with an RDK that alternated between leftward motion in front and rightward motion behind. To prevent eye movements, two such movies were presented out of phase, above and below fixation. We found that observers' biases for which direction of motion moved in front were different between the pre- and post-adaptation sessions, in a manner mostly consistent with a depth contingent motion after-effect. These results emphasize the critical role of neural structures sensitive to both motion and binocular disparity in the perception of motion transparency.

7.3 General Issues & Evaluation of technique

The critical finding here is that the variations in perception following adaptation can be accurately tracked in such a way that individual differences in response to adaptation can be measured. Previous research has primarily focused on a button press or verbal report that indicates the end of the after-effect. This was often taken as a measure of the after-effect strength. The data presented here indicates that both the strength *and* duration can be measured following adaptation. This gives a clearer picture of the temporal variation of after-effects in the area of motion and depth. It also offers a method of estimating the strength of the after-effect at time zero (assuming the decay function of the after-effect), and gives an estimate of the end of the effect.

The results are different for depth and motion in terms of individual variation in the strength of the after-effect (in percentage terms). It is often suggested, although to our knowledge not explicitly demonstrated, that there is more individual variation in stereoscopic depth perception than in motion perception (see Coutant & Westheimer, 1993 and Van Ee & Richards, 2002 for studies of individual variation in stereopsis). These results provide a confirmation of this "psychophysical folklore" although there are issues to do with stimulus complexity which are clearly also factors.

The emergence of this method is timely given the emergence of new theoretical understanding of the functional significance of adaptation. This is correlated with a movement in the literature towards adaptation having a more complex explanation than mere neuronal fatigue. When aiming to understand complex interacting mechanisms, a method of assessing how these mechanisms interact over time must give better insight into the processes involved.

A precise example of the reason for this is that if you wish to measure the impact of nulling one depth cue with another, the decay in each cue would need to be addressed for individual observers in each cue prior to adaptation. To establish the interaction from the two cues, this temporal variation pre- and post-adaptation could be compared. Also, the initial value for participants could be measured.

As has been mentioned, the technique provides a method for capturing the temporal dynamics of after-effects, which can be depicted in terms of duration and magnitude. However, there are criticisms of the technique which are presented here.

Evaluation of technique

Utilising this technique it is predicted that a change in the time taken to reach a perceptual reversal of the stimulus will change with the test condition. Thus, with reference to the depth after-effect, given the hypothesis that increasing disparity causes increased depth, a longer time constant is expected given a lower test disparity. This is indeed what we report. The interpretation we offer of this though is that the increased disparity is leading to rapid nulling of the depth after-effect, given a shorter time constant.

An issue raised by this technique is that response bias could be a major factor occurring during the testing period. This simply means that the participants learned to respond in a certain way for a period of time during the testing period, then, when a reversal was perceived, they responded in the other direction. This change then simply correlated with different test conditions.

There are two reasons why it is unlikely that this occurred. First of all, the test conditions were presented in a random order. Participants were unaware of which test condition they were in, thus could not predict the shift of the reversal that should be predicted. If participants were consciously or subconsciously accounting for their responses by saying ‘I’ll respond in this direction for a period of time, then switch to another’, increasing duration time (given by perceptual reversal time) would increase with test order presentation. This differed between participants, but in nearly every experiment conducted the time to reach perceptual reversal correlated with increasing nulling ‘energy’.

However, an improvement that could be implemented to the technique in future lines of research is to introduce 'catch' *trials into the testing period. With reference to* measuring the depth after-effect for instance, during the testing period after a few seconds a larger disparity could be presented and the response checked to see if people are indeed responding to the stimulus during the testing period.

A further possibility is to completely randomise within the testing period the conditions that are being presented. This would mean adapting people for a period of time and then presenting them with various disparities/velocity and checking the perception of the after-effect. This is a possibility for future lines of research.

One limitation of this technique does not allow for the quantification of all types of after-effect. For example, the static after-effect remains extremely difficult to quantify. It is extremely difficult to know which stimulus parameter to vary during the nulling period. For instance, in this thesis we measured the movement after-effect using velocity as the nulling parameter. Thus, with increasing velocity a shorter duration of after-effect was found. However, the relationship between velocity coding and the strength *of the after-effect is still* unresolved. Indeed, explicit assumptions about velocity coding are not built into models of the MAE, they instead largely rely on direction coding (Mather & Harris, 1998). It is interesting in the experiments reported here that we did indeed find individual variation, however, for the vast majority an increase in velocity did lead to a decrease in the duration of the after-effect. Further testing over a range of values would reveal a more explicit relationship between velocity coding and MAE.

Overall, the technique provides a window into the temporal dynamics of after-effects. This technique is similar in spirit to that of Hershenson (1989) but provides a more objective measurement of the participants change in perception (they employ a verbal rating scale). We applied this technique in visual after-effects and have reported the findings in relation to motion and depth.

7.4 Future lines of research and potential applications

We suggest two main lines for future research. One issue is to incorporate the temporal dynamics of after-effects of other cues with a view to understanding the establishment of the level of interaction of cues and the other is to extend current models of adaptation.

Different after-effects & cue interaction

The technique presented in Chapters 3, 4 & 5 demonstrates a novel method for capturing the temporal dynamics of after-effects. This could be applied in the analysis of other after-effects. A good example here would be in monitoring the time course of colour after-effects or orientation after-effects.

Following application of this technique is other areas, it would then be possible to address the level at which the different cues in the visual system interact. Research thus far has been concerned with the interaction of cues when cues are close to each other and providing depth (e.g. Landy et al, 1995). In contrast to this approach a more direct test of cue interaction in depth perception can be achieved by trying to *null* depth specified by one cue with another. This is a useful technique and application of it has already resulted in findings about the interaction of cues and depth perception (Bradshaw et al, 2000). Therefore, information on the level of the interaction could be tested. In the case of using a different combination of cues, this technique would allow for the accurate recording of the immediate strength of the after-effect at time zero and also how the after-effect is varying in time, for any cue. Given that the weight attached to any cue can change with the available information in a situation, the underlying plasticity of the system could reflect different adaptive mechanisms with different time courses. This could explain the recalibration process that is suggested to underlie adaptation or 'cue promotion' (Haijiang et al, 2006).

Underlying mechanisms

Having developed this technique and obtained these results, this provides a new set of data in which to research the underlying mechanisms of adaptation. From these results it is also clear that there are potentially different mechanisms underlying that of motion and depth adaptation processing in the visual system. In order to capture this difference it is necessary to develop an underlying framework for understanding adaptation. The output from the thesis gives a strong platform on which to build this, as we have developed an accurate way of measuring the after-effects. For example, the data-set could be used to extend current models of adaptation (see Wainright

(1999)) to consider the time-course of adaptation. One issue is that in applying this model to both the disparity and motion data, it is clear that the same model cannot account for both. In the case of motion, the after-effect obtained is very much dependent on the characteristics of the test stimuli used (which is unlike the results obtained for the depth after-effect). With the results obtained for motion perception, the effect appears to be sharply tuned, with the strongest effect occurring when the similarity is greatest between adaptation and test. It has been hypothesised that there are not one but two temporal channels in the visual system, one sensitive to low spatial frequency, the other to high. The existence of two after-effects has also been used to argue that there are two sites involved in processing of motion, due to the fact that two different types of after-effect can be elicited. One interesting question here would be to establish a model which can account for this difference, through varying the parameters from the data on the depth after-effect to that obtained for the different experiments in motion, and to account for this difference through consideration of information encoding. Following this, a straightforward extension would be the development of the studies on contingent after-effects, which has applications in terms of learning associations.

Wider Applications

Learning and conditioned behaviour

It is estimated that 230,000 / 350,000 people have severe learning disabilities in the UK (http://www.learningdisabilities.org.uk). This is a serious problem, as this can then impact on self-esteem and social functioning, and can often lead to social exclusion. Relevant to the understanding of learning is the process of adaptation which can be seen as a type of implicit procedural learning (Fernández-Ruiz, 1999). Looking at learning within this framework can be particularly useful as it provides a method of looking at the quick recalibration of the visual system, where exposure to different cues in the environment can enhance learning even after short periods (an example being the new idea of 'cue recruitment' (Haijiang et al, 2006)). Is it a possibility that adaptation could be manipulated to enhance learning? Improvement in areas such as learning disabilities will benefit society in general, where social stigma attached to problems in learning difficulties is very high. Understanding the nature of adaptation in detail and also the relation between adapting signals, could provide a significant step in helping those with learning problems.

Clinical Research

Adaptation is often used as a non-invasive measure of investigating properties of the brain. It is often said, 'if it adapts, it is there' (Mollon, 1974). Clinical studies therefore use this phenomenon to look at differences in known clinical groups, to try and infer underlying neural problems. However, most methods for measuring the degree of adaptation use measures that access only one dimension of the after-effect. The present research examined the temporal aspects of after-effects and worked on developing a technique that captured not only the time duration but also the strength of adaptation to a given stimulus. The development of this research could therefore enhance the specificity of the adaptation measure, allowing for more accurate comparison of clinical and control groups. This could lead to more accurate location of underlying mechanisms of the specific problem.

Industrial applications

Engineers often need to know exact quantities, for example, how much light is needed for a sign to be visible to drivers. This research has focused on the change in response of the visual system over time, with what could be argued is a more accurate measure than has been employed previously. Being able to disseminate findings on the temporal aspects of these processes therefore has potential industrial applications.

Academic research

It is important to try to investigate the nature of the mechanisms underlying adaptation. As more complex theories emerge to try and explain the phenomena, it is important to achieve accuracy in the measurement in the state changes of the system in response to the environment. This thesis developed a technique for achieving this and applied it to two areas in vision.

7.5 Conclusions

Based on the research presented here, it is possible to draw conclusions about the nature of adaptation and after-effects in the system.

Critically, we captured the full temporal variation of the after-effect through the development of a novel technique. This technique allows the inference of the strength of the after-effect at time zero, and gives an objective method of estimating the end of the effect. Following development of this technique, we applied this in the area of both motion and depth.

In terms of the depth after-effect, it appears that there is great individual observer variability in the relation between depth and disparity. This is consistent with reports of widespread stereo anomaly (Van Ee & Richards, 2002). In investigating the movement after-effect, the most striking finding is the difference between the type of test used in the perception of the after-effect. Our studies support the proposal that different sites underlie the range of adaptation effects reported. In generating an after-effect, our results suggest that adaptation duration and test speed are important determining factors.

Finally, in the last chapter of this thesis we investigated the influence of prior adaptation to the perception of transparency. Despite variation in the after-effect recorded for both depth and motion individually, it was found that when adapted together, this influenced viewing of a transparent surface. This indicates adaptability across what is being stimulated at the time to possible higher-level effects. This could be likened to learning.

We extend current findings by demonstrating that adaptation to non-transparent motion and disparity can also influence the perception of transparent stimuli. We find that participants' perceptions of ambiguous stimuli were influenced by adaptation contingent with the predicted after-effect, despite the lack of adaptation to a transparent surface. This result again highlights the importance of neural structures tuned to both disparity and direction.

Appendix 1.

A possibility when investigating the effect of a Depth Contingent Motion After-Effect (DCMAE) on observers' bias for depth ordering, as is presented in Chapter 6, is that the influence of the after-effect may have decayed throughout the testing period. To check for the dissipation of after-effects due to the lack of a topping up procedure in the experiment, the trials were split into those occurring in the first half of the testing session and those occurring in the second half. This was carried out for the pre-adaptation session and the post-adaptation session. This gives four conditions, which we have termed: Pre-Early, Pre-Late, Post-early, Post-Late. The mean of these values for all subjects is shown in Figure 1.

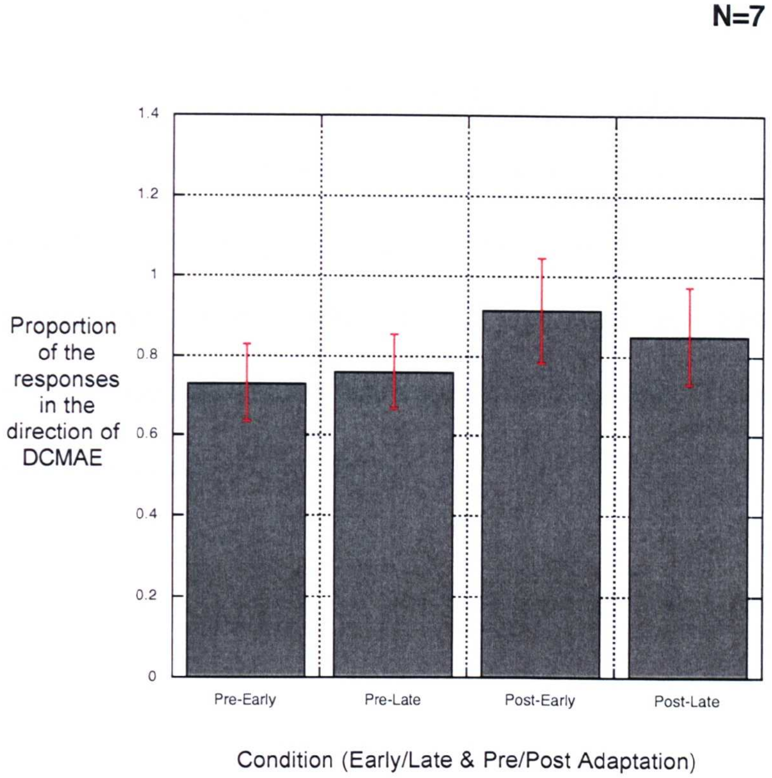

Figure 1. Graph to show average response bias obtained for all subjects according to time of the test (Early versus Late) and state of adaptation (Pre versus Post). Bars indicate standard error of mean.

A comparison of the means shown in Figure 1 revealed a significant difference between Pre-Early/Late and Post-Early conditions (df=6, t=2.6, $p<.05$, df=6,t=3.375, $p<0.01$: one tailed) but no significant difference when comparing Pre-Early/Late with Post-Late conditions (the trials occurring in the second half of the testing session). This indicated that the influence of the after-effect was greatest in the first half of the testing session following adaptation. The influence of the DCMAE on observers' interpretation of the depth order of a transparent surface is greatest in the time period immediately following adaptation. If investigating the temporal dynamics of this influence, a topping up procedure should be implemented to prevent decay of the effect. In the current experiment this was not the aim (as we wished to investigate the modifiability of any bias present for the interpretation of motion and disparity information). However, in experiments investigating the temporal dynamics of the influence of the after-effect a topping up procedure would be implemented.

References

Addams, R. (1834). "An account of a peculiar optical phaenomenon seen after having looked at a moving body." London and Edinburgh Philosophical Magazine and Journal of Science 5,: 373-374.

Alais, D., M. J. van der Smagt, et al. (1996). "Monocular mechanisms determine plaid motion coherence." Vis Neurosci 13(4): 615-26.

Anstis, S., F. A. J. Verstraten, et al. (1998). "The motion aftereffect." Trends in Cognitive Sciences 2(3): 111-117.

Anstis, S. M. and J. P. Harris (1974). "Movement aftereffects contingent on binocular disparity." Perception 3(2): 153-68.

Anstis, S. M. and Duncan., K. (1983). "Separate motion aftereffects from each eye and from both eyes." Vision Res 23: 161-169.

Ashida, H. and N. Osaka (1994). "Difference of spatial frequency selectivity between static and flicker motion aftereffects." Perception 23(11): 1313-20.

Ashida, H. and N. Osaka (1995). "Motion aftereffect with flickering test stimuli depends on adapting velocity." Vision Res 35(13): 1825-33.

Bach, M., M. Hoffmann, et al (1996). "Motion-onset VEP: Missing direction-specificity of adaptation?" Investigative Opthamology and Visual Science 37 (Suppl.):: 446.

Baker, C. L., Jr. and O. J. Braddick (1982). "The basis of area and dot number effects in random dot motion perception." Vision Res 22(10): 1253-9.

Barlow, H. B., Ed. (1990). A theory about the functional role and synaptic mechanism of after-effects. Vision: Coding and Efficiency (Cambridge:),. Cambridge, Cambridge Univ. Press.

Barlow, H. B. (1997). "The knowledge used in vision and where it comes from." Philosophical Transactions of the Royal Society of London Series B-Biological Sciences 352(1358): 1141-1147.

Barlow, H. B. (1997). "The knowledge used in vision and where it comes from." Philosophical Transactions of the Royal Society of London Series B-Biological Sciences 352(1358): 1141-1147.

Barlow, H. B. and R. M. Hill (1963). "Evidence for a Physiological Explanation of the Waterfall Phenomenon and Figural after-Effects." Nature 200: 1345-7.

Barlow, H. B. M., J. D. (1982). The Senses. Cambridge, Cambridge University Press.

Berardi, N. F., A. (1981). "Perceptual Learning in a grating discrimination task is specific for orientation and spatial frequency." Behavioural Brain Research 2(2): 243-244.

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." J Physiol 203(1): 237-60.

Blakemore, C. and F. W. Campbell (1969). "Adaptation to spatial stimuli." J Physiol 200(1): 11P-13P.

Blakemore, C. and B. Julesz (1971). "Stereoscopic depth aftereffect produced without monocular cues." Science 171(968): 286-8.

Blakemore, C. and R. Over (1974). "Curvature detectors in human vision?" Perception 3(1): 3-7.

Blakemore, C. and P. Sutton (1969). "Size adaptation: a new aftereffect." Science 166(902): 245-7.

Bradley, D. C., N. Qian, et al. (1995). "Integration of motion and stereopsis in middle temporal cortical area of macaques." Nature 373(6515): 609-11.

Bradshaw, M. F., A. D. Parton, et al. (2000). "The task-dependent use of binocular disparity and motion parallax information." Vision Res 40(27): 3725-34.

Brainard, D. H. (1997). "The Psychophysics Toolbox." Spatial Vision 10: 433-436.

Bulakowski, P. K., K, Liang, J & David Whitney (2006). Independent coding of object motion and position revealed by distinct contingent aftereffects. Journal of Vision, 6, 550a.

Cameron, E. L., C. L. Baker, Jr., et al. (1992). "Spatial frequency selective mechanisms underlying the motion aftereffect." Vision Res 32(3): 561-8.

Carandini, M., H. B. Barlow, et al. (1997). "Adaptation to contingencies in macaque primary visual cortex." Philos Trans R Soc Lond B Biol Sci 352(1358): 1149-54.

Carandini, M. and D. Ferster (1997). "A tonic hyperpolarization underlying contrast adaptation in cat visual cortex." Science 276(5314): 949-52.

Carlson, V. R. (1962). "Adaptation in the perception of visual velocity." J. Exp. Psychol. 64: 192-197.

Castet, E., D. R. Keeble, et al. (2002). "Nulling the motion aftereffect with dynamic random-dot stimuli: limitations and implications." J Vis 2(4): 302-11.

Chaudhuri, A. (1990). "Modulation of the motion after-effect by selective attention." Nature 344(6261): 60-2.

Clifford, C. W. and G. Rhodes (2005). Fitting the Mind to the World: Adaptation and Aftereffects in High-Level Vision. USA, OUP.

Coutant, B. E. and G. Westheimer (1993). "Population distribution of stereoscopic ability." Ophthalmic Physiol Opt 13(1): 3-7.

Culham, J. N., S. Ledgeway, T. Cavanagh, P. von Grunau, M. Kwas, M. Alias, D & Raymond, J. (1998). Higher-Order Effects. The Motion After-effect: A Modern Perspective. F. V. S. A. E. Mather. Cambridge, MA, MIT Press.

Derrington, A. M. and P. Lennie (1982). "The influence of temporal frequency and adaptation level on receptive field organization of retinal ganglion cells in cat." J Physiol 333: 343-66.

Durgin, F. H. (1996). "Visual aftereffect of texture density contigent on color of frame." Percept Psychophys 58(2): 207-23.

Erkelens, C. J. and R. van Ee (1998). "A computational model of depth perception based on headcentric disparity." Vision Res 38(19): 2999-3018.

Fang, F. H., S. (2004). "Strong influence of test patterns on the perception of motion aftereffect and position." Journal of Vision 4(7): 637-42.

Fernandez-Ruiz, J. and R. Diaz (1999). "Prism adaptation and aftereffect: specifying the properties of a procedural memory system." Learn Mem 6(1): 47-53.

Fiorentini, A. and N. Berardi (1980). "Perceptual learning specific for orientation and spatial frequency." Nature 287(5777): 43-4.

Fox, R. (1982). "Effect of depth position on the motion aftereffect." Investigative Opthamology and Visual Science 22: 144.

Frisby, J. P. (1979). Seeing, Illusion, Brain and Mind. Oxford, Oxford University Press.

Giaschi, D., R. Douglas, et al. (1993). "The time course of direction-selective adaptation in simple and complex cells in cat striate cortex." J Neurophysiol 70(5): 2024-34.

Gibson, J. J. and E. J. Gibson (1955). "Perceptual learning; differentiation or enrichment?" Psychol Rev 62(1): 32-41.

Goldstein, E. B. (2007). Sensation & Perception. Pacific Grove, CA., Wadsworth Pub. Co.

Goldstone, R. L. (1998). "Perceptual learning." Annu Rev Psychol 49: 585-612.

Graham, M. and B. Rogers (1982). "Simultaneous and successive contrast effects in the perception of depth from motion-parallax and stereoscopic information." Perception 11(3): 247-62.

Graham, N. V. S. (1989). Visual pattern analyzers. Oxford, Oxford University Press.

Haijiang, Q., J. A. Saunders, et al. (2006). "Demonstration of cue recruitment: change in visual appearance by means of Pavlovian conditioning." Proc Natl Acad Sci U S A 103(2): 483-8.

Hammett, S.T., Snowden, R.J. and Smith, A.T. (1993). “Perceived contrast as a function of adaptation duration.” Vision Research, 34, 31-40

Hammond, P., B. Ahmed, et al. (1986). "Relative motion sensitivity in cat striate cortex as a function of stimulus direction." Brain Res 386(1-2): 93-104.

Hammond, P., C. J. Pomfrett, et al. (1989). "Neural motion after-effects in the cat's striate cortex: orientation selectivity." Vision Res 29(12): 1671-83.

Harris, L. R., M. J. Morgan, et al. (1981). "Moving and the motion after-effect." Nature 293(5828): 139-41.

Hershenson, M. (1989). "Duration, time constant, and decay of the linear motion aftereffect as a function of inspection duration." Percept Psychophys 45(3): 251-7.

Hershenson, M. (1993). "Linear and rotation motion aftereffects as a function of inspection duration." Vision Res 33(14): 1913-9.

Howard, I. P. and B. J. Rogers (2002). Seeing in Depth. Toronto, University of Toronto Press.

Hubel, D. H. and T. N. Wiesel (1962). "Receptive fields, binocular interaction and functional architecture in the cat's visual cortex." J Physiol 160: 106-54.

Hughes, B., W. Epstein, et al. (1990). "An asymmetry in transmodal perceptual learning." Percept Psychophys 48(2): 143-50.

Jones, P. D. and D. H. Holding (1975). "Extremely long-term persistence of the McCollough effect." J Exp Psychol Hum Percept Perform 1(4): 323-7.

Kanai, R. and F. A. Verstraten (2005). "Perceptual manifestations of fast neural plasticity: motion priming, rapid motion aftereffect and perceptual sensitization." Vision Res 45(25-26): 3109-16.

Keck, M. J. and B. Pentz (1977). "Recovery from adaptation to moving gratings." Perception 6(6): 719-25.

Koenig, E. and J. Dichgans (1981). "Aftereffects of vestibular and optokinetic stimulation and their interaction." Ann N Y Acad Sci 374: 434-45.

Kohler, I. (1964). The formation and transformation of the perceptual world. New York, International Universities Press.

Kohler, W. and D. A. Emery (1947). "Figural aftereffects in the third dimension of visual space." Am J Psychol 60: 159-201.

Kohn, A. and J. A. Movshon (2004). "Adaptation changes the direction tuning of macaque MT neurons." Nat Neurosci 7(7): 764-72.

Landy, M. S., L. T. Maloney, et al. (1995). "Measurement and modeling of depth cue combination: in defense of weak fusion." Vision Res 35(3): 389-412.

Lankheet, M. J. and F. A. Verstraten (1995). "Attentional modulation of adaptation to two-component transparent motion." Vision Res 35(10): 1401-12.

Ledgeway, T. and A. T. Smith (1997). "Changes in perceived speed following adaptation to first-order and second-order motion." Vision Res 37(2): 215-24.

Lee, B. (1999). "Aftereffects and the representation of stereoscopic surfaces." Perception 28(9): 1155-69.

Lehmkuhle, S. and R. Fox (1977). Stereoscopic Motion Aftereffects. Midwestern Psychological Assocaition, Chicagp.

Linden, D. E., U. Kallenbach, et al. (1999). "The myth of upright vision. A psychophysical and functional imaging study of adaptation to inverting spectacles." Perception 28(4): 469-81.

Liu, J. and W. T. Newsome (2003). "Functional organization of speed tuned neurons in visual area MT." J Neurophysiol 89(1): 246-56.

Long, N. and R. Over (1973). "Stereoscopic depth aftereffects with random-dot patterns." Vision Res 13(7): 1283-7.

Maffei, L., A. Fiorentini, et al. (1973). "Neural correlate of perceptual adaptation to gratings." Science 182(116): 1036-8.

Mamassian, P. and J. Wallace (2003). "Depth assignment in motion transparency." Journal of Vision 3(9): 805.

Mareschal, I., H. Ashida, et al. (1997). "Linking lower and higher stages of motion processing?" Vision Res 37(13): 1755-9.

Mather, G. (1980). "The movement aftereffect and a distribution-shift model for coding the direction of visual movement." Perception 9(4): 379-92.

Mather, G. (1991). "First-order and second-order visual processes in the perception of motion and tilt." Vision Res 31(1): 161-7.

Mather, G. and J. Harris (1998). Theoretical models of the motion aftereffect. The Motion Aftereffect: A Modern Perspective. G. Mather, F. A. Verstraten and S. Anstis. Cambridge, Massachusetts, MIT.

Maddess, T. Dubois, R. A and Ibbotson, M (1991). “Response properties and adaptation of neurons sensitive to image motion in the butterfly Papillo aegeus”. J Exp Biol (161):171-199.

Maddess, T. And Laughlin, S. B. (1985). Adaptation of the motion sensitive neuron H1 is generated locally and governed by Contrast frequency. Proc Roy Soc Lon B.(225):251-275.

Mather, G. and B. Moulden (1980). "A simultaneous shift in apparent direction: further evidence for a "distribution-shift" model of direction coding." Q J Exp Psychol 32(2): 325-33.

Mather, G., F. A. Verstraten, et al. (1998). The Motion Aftereffect: A Modern Perspective. Cambridge, Massachusettes., MIT Press.

Mayhew, J. E. and H. C. Longuet-Higgins (1982). "A computational model of binocular depth perception." Nature 297(5865): 376-8.

McArthur, K. and P. Mamassian (2005). "Temporal dynamics of bistability in motion transparency." Journal of Vision 5(8): 701.

McCollough, C. (1965). "The Conditioning of Color-Perception." Am J Psychol 78: 362-78.

Mitchell, D. E. and A. G. Baker (1973). "Stereoscopic aftereffects: evidence for disparity-specific neurones in the human visual system." Vision Res 13(12): 2273-88.

Mollon, J. D. (1974). "Aftereffects and the Brain." New Scientist 61(479-482).

Mollon, J. D. and Polden, P. G. (1980). A curiosity of light adaptation. Nature, 286, 59-62.

Mollon, J. D. (1982). "Color vision." Annu Rev Psychol 33: 41-85.

Movshon, J. A. and P. Lennie (1979). "Pattern-selective adaptation in visual cortical neurones." Nature 278(5707): 850-2.

Nishida, S. and H. Ashida (2000). "A hierarchical structure of motion system revealed by interocular transfer of flicker motion aftereffects." Vision Res 40(3): 265-78.

Nishida, S. and H. Ashida (2001). "A motion aftereffect seen more strongly by the non-adapted eye: evidence of multistage adaptation in visual motion processing." Vision Res 41(5): 561-70.

Nishida, S., H. Ashida, et al. (1994). "Complete interocular transfer of motion aftereffect with flickering test." Vision Res 34(20): 2707-16.

Nishida, S., H. Ashida, et al. (1997). "Contrast dependencies of two types of motion aftereffect." Vision Res 37(5): 553-63.

Nishida, S., M. Edwards, et al. (1997). "Simultaneous motion contrast across space: Involvement of second-order motion?" Vision Research 37(2): 199-214.

Nishida, S. and T. Sato (1995). "Motion aftereffect with flickering test patterns reveals higher stages of motion processing." Vision Res 35(4): 477-90.

Nishida, S. S., T. (1992). "Positive motion aftereffect induced by bandpass filtered random-dot kinematograms." Vision Research 32: 1635-46.

Ohzawa, I., G. Sclar, et al. (1982). "Contrast gain control in the cat visual cortex." Nature 298(5871): 266-8.

Over, R., J. Broerse, et al. (1973). "Spatial determinants of the aftereffect of seen motion." Vision Res 13(9): 1681-90.

Pantle, A. (1998). How Do Measures of the Motion Aftereffect Measure Up? The Motion Aftereffect: A Modern Perspective. G. Mather, F. A. Verstraten and S. Anstis. Cambridge, Massachusetts., The MIT Press.: 25-40.

Pantle, A., S. Lehmkuhle, et al. (1978). "On the capacity of directionally selective mechanisms to encode different dimensions of moving stimuli." Perception 7(3): 261-7.

Pantle, A. J. (1978). "Temporal frequency response characteristic of motion channels measured with three different psychophysical techniques." Percept Psychophys 24(3): 285-94.

Pelli, D. G. (1997). "The VideoToolbox software for visual psychophysics: Transforming numbers into movies." Spatial Vision 10: 437-442.

Pelli, D. G. (1997). "The VideoToolbox software for visual psychophysics: transforming numbers into movies." Spat Vis 10(4): 437-42.

Recanzone, G. H. (1998). "Rapidly induced auditory plasticity: The ventriloquism aftereffect." Proceedings of the National Academy of Science 95: 869-75.

Rhodes, G., L. Jeffery, et al. (2003). "Fitting the mind to the world: face adaptation and attractiveness aftereffects." Psychol Sci 14(6): 558-66.

Rhodes, G., L. Jeffery, et al. (2004). "Orientation-contingent face aftereffects and implications for face-coding mechanisms." Curr Biol 14(23): 2119-23.

Rogers, B. and M. Graham (1982). "Similarities between motion parallax and stereopsis in human depth perception." Vision Res 22(2): 261-70.

Rose, D., M. F. Bradshaw, et al. (2003). "Attention affects the stereoscopic depth aftereffect." Perception 32(5): 635-40.

Rose, D. and E. Price (1995). "Functional separation of global and local stereopsis investigated by cross-adaptation." Neuropsychologia 33(3): 269-74.

Saul, A. B. and M. S. Cynader (1989). "Adaptation in single units in visual cortex: the tuning of aftereffects in the temporal domain." Vis Neurosci 2(6): 609-20.

Smith, R. A., Jr. (1976). "The motion/disparity aftereffect: a preliminary study." Vision Res 16(12): 1507-9.

Sohn, W. and A. E. Seiffert (2006). "Motion aftereffects specific to surface depth order: beyond binocular disparity." J Vis 6(2): 119-31.

Spigel, I. M. (1960). "The effects of differential post-exposure illumination on the decay of the movement after-effect." Journal of Psychology 50: 209-210.

Spigel, I. M. (1962). "CFF and surrounds of simultaneous contrast." Percept Mot Skills 15: 275-81.

Stratton, G. M. (1896). "Some preliminary experiments on vision without the inversion of the retinal image." psychological review 3: 611-17.

Stratton, G. M. (1897c). "Vision without inversion of the retinal image." Psychological Review 4: 463-81.

Sutherland, N. S. (1961). "Figural aftereffects and apparent size." Quaterly Journal of Experimental Psychology 13: 222-228.

Swanston, M. T. and N. J. Wade (1992). "Motion over the retina and the motion aftereffect." Perception 21(5): 569-82.

Taya, S., M. Sato, et al. (2005). "Stereoscopic depth aftereffects without retinal position correspondence between adaptation and test stimuli." Vision Res 45(14): 1857-66.

Tebartz van Elst, L., Greenlee, MW, A Foley, JM, Lucking, CH (1997). "Contrast detection, discrimination and adaptation in patients with Parkinson's disease and multiple system atrophy." Brain 120(12): %P 2219-2228.

Thompson, P. (1981). "Velocity after-effects: the effects of adaptation to moving stimuli on the perception of subsequently seen moving stimuli." Vision Res 21(3): 337-45.

Thompson, P. (1998). Tuning of the Motion Aftereffect. The Motion Aftereffect: A Modern Perspective. G. Mather, F. A. Verstraten and S. Anstis. Cambridge, Massachusetts, MIT: 41-56.

Thompson, P. and J. Wright (1994). "The role of intervening patterns in the storage of the movement aftereffect." Perception 23(10): 1233-40.

van de Grind, W. A., van Hof, P., van der Smagt, M. J., & Verstraten, F. A. J. (2001). "Slow and fast visual motion channels have independent binocular rivalry stages." Proceedings of the Royal Society, London B. 268: 437-443.

van de Grind, W. A., F. A. Verstraten, et al. (1994). "Ensemble models of the movement aftereffect and the influence of eccentricity." Perception 23(10): 1171-9.

van der Smagt, M. J., Verstraten, F. A. J., & van de Grind, W. A. (1999). "A new transparent motion after-effect [letter]." Nature Neuroscience 2: 595-6.

van Ee, R. and W. Richards (2002). "A planar and a volumetric test for stereoanomaly." Perception 31(1): 51-64.

Van Wezel, R. J. and K. H. Britten (2002). "Motion adaptation in area MT." J Neurophysiol 88(6): 3469-76.

Verstraten, F. A., R. E. Fredericksen, et al. (1996). "Directional motion sensitivity under transparent motion conditions." Vision Res 36(15): 2333-6.

Verstraten, F. A., M. J. van der Smagt, et al. (1998). "Aftereffect of high-speed motion." Perception 27(9): 1055-66.

Verstraten, F. A., R. Verlinde, et al. (1994). "A transparent motion aftereffect contingent on binocular disparity." Perception 23(10): 1181-8.

Verstraten, F. A. J., Fredericksen, R E, Van Wezel, R. J., Lankheet, M. J. & Van de Grind, W. A. (1996). "Recovery from adaptation for dynamic and static motion aftereffects: Evidence for two mechanisms." Vision Research 36: 421-424.

Verstraten, F. A. J. v. d. S., M. J., Frederickson, R. E., & van de Grind, W. A. (1999). "Integration after adaptation to transparent motion: static and dynamic test patterns result in different aftereffect directions." Vision Research 39: 803-10.

Wade, N. J. (1994). "A selective history of the study of visual motion aftereffects." Perception 23(10): 1111-34.

Wade, N. J. and F. A. Verstraten (2005). Accommodating the past: a selective history of adaptation. Fitting the Mind to the World: Adaptation and Aftereffects in High-Level Vision. C. W. Clifford and G. Rhodes, OUP. 2.

Wade, N. J. S., L., Swanston, M. T. (1996). "Visual motion after-effects: Critical adaptation and test conditions." Vision Research 36: 2167-75.

Wade, N. J. S.-P., V. (1998). "Visual motion after-effects: differential adaptation and test stimulation." Vision Research 38: 573-8.

Wade, N. J. S.-P., V. (1998). "Visual motion aftereffects: differential adaptation and test stimulation." Vision Res 38(4): 573-8.

Wainwright, M. J. (1999). "Visual adaptation as optimal information transmission." Vision Research 39(23): 3960-3974.

Wiesenfelder, H. and R. Blake (1992). "Binocular rivalry suppression disrupts recovery from motion adaptation." Vis Neurosci 9(2): 143-8.

Wohlegemuth, A. (1911). "On the after-effect of seen movement." British Journal pf Psychology (Supp) 1: 1-117.

Wright, M. J. and A. Johnston (1985). "Invariant tuning of motion aftereffect." Vision Res 25(12): 1947-55.