THE EFFECT OF DISRUPTING THE HUMAN MAGNOCELLULAR PATHWAY ON GLOBAL MOTION PERCEPTION

by

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Abstract

Purpose: To determine the effect of human magnocellular (M) pathway disruption on global motion perception. *Method:* Thirty adults completed a global motion task under four conditions. The task was completed after adaptation to full-field sinusoidal flicker (experimental condition #1), after adaptation to a gray field (control condition #1), in the presence of a red background (experimental condition #2) and in the presence of a gray background (control condition #2). Based on lesion studies and the physiological properties of single cells in the subcortical M pathway, it was predicted that the psychophysical techniques use in both experimental conditions would disrupt normal functioning of this pathway and result in elevated motion coherence thresholds. *Results:* Adaptation to flicker and the presence of a red background increased motion coherence thresholds. The threshold elevation was greater when participants were adapted to flicker. *Conclusion:* Flicker adaptation and the presence of a red background are assumed to temporarily disrupt the M pathway at a subcortical level. The fact that these techniques elevate motion coherence thresholds suggests that the subcortical M pathway is needed for normal human motion perception.

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Findings from both monkey and human research have led to general agreement that beginning in the retina, the visual system can be considered to be composed of at least two main parallel and complementary pathways: the magnocellular (M) and parvocellular (P) pathways (Shapley, 1990). The M pathway ultimately provides the major input into a visual cortical area called V5 or MT in the vicinity of the temporoparietaloccipital junction (Merigan & Manusell, 1993). This cortical area is considered the location where motion information is integrated, thereby allowing for motion perception (Maunsell & Newsome, 1987). Studies have shown that a lesion to a monkey's subcortical M pathway (Merigan, Byrne & Maunsell, 1991; Merigan & Manusell, 1993) or a similar lesion-like disruption to the M pathway caused by either optic neuritis (Barton & Rizzo, 1994) or glaucoma (Silverman, Trick & Hart, 1990) in humans, results in a decreased ability to perceive motion. These findings led to the assumption that the human M pathway carries motion information to V5/MT. The problem with this assumption is that these studies have examined monkeys or humans with brain damage and it is therefore not clear what to conclude about normal human motion perception. Furthermore, subcortical neurons are not sensitive to motion (Van Essen & De Yoe, 1995). The goal of this study was to investigate whether selective disruption of the subcortical M pathway, caused by two psychophysical techniques, interferes with normal motion perception in humans.

Global Motion Perception

Combining psychophysical and physiological research findings in the study of motion perception has led to significant progress in understanding the neural correlates that mediate this behaviour (Movshon & Newsome, 1992). One behavioural task, called a global motion task, has often been used in bridging these two respective fields of research when studying motion perception in monkeys and humans. The stimulus of a typical global motion task consists of many random white dots that appear on a computer screen with a black background. On each trial a certain proportion of the dots move coherently in one direction (i.e., left or right). The remaining dots move in random directions. A participant's task is to decide the direction in which the coherently moving dots are moving. When the coherence value is varied according to one of the psychophysical methods a coherence threshold can be determined. This threshold indicates the proportion of dots that must be moving coherently in order for participants to accurately discriminate the direction of motion. A lower coherence threshold is therefore indicative of better performance on a global motion task. Newsome and Pare (1988) showed that a lesion to cortical area V5/MT in monkeys caused a significant elevation in coherence thresholds. Human brain lesions have provided evidence that there is a cortical area functionally equivalent to V5/MT in humans, which is located in the vicinity of the temporoparietaloccipital junction (Schenk & Zihl, 1997). The motion perception deficit

that results from these lesions shows that cortical area V5/MT is needed for global motion perception. V5/MT holds the ability to integrate motion signals across a large portion of the visual field to attain a percept of the direction of global motion within a random-dot field (Schenk & Zihl, 1997).

Parallel Visual Pathways: The M and P Pathways

As previously mentioned, the human visual system is considered to be composed of at least two pathways, the M and P pathways. These two pathways are shown in Figure 1. The M pathway's anatomical and physiological properties will be reviewed because of their relevance to the current study. A brief review of P pathway physiology will ensure that the functional separation of these pathways is well understood and that the role of the M pathway in visual perception is emphasized.

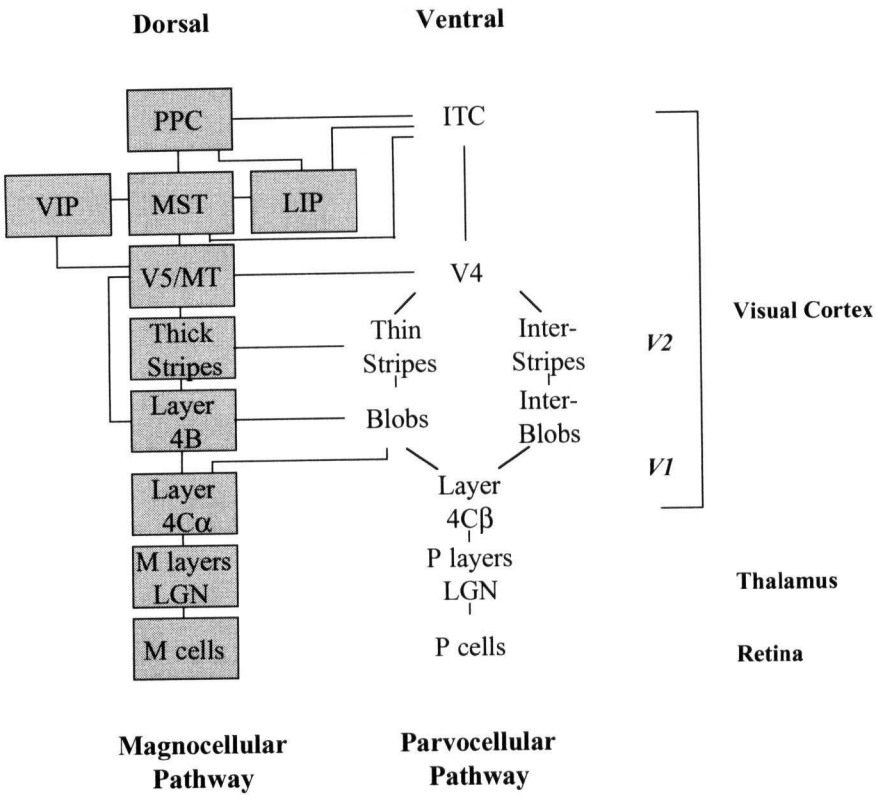

Figure 1. Parallel pathways in the primate visual system (From Edwards et al., 2003). Abbreviations in this figure: M, magno; P, parvo; MT, middle temporal area; VIP, ventral intraparietal area; MST, medial superior temporal area; LIP, lateral intraparietal area; PPC, posterior parietal cortex; ITC, inferior temporal cortex.

Anatomical and Physiological Properties of the Subcortical Visual Pathways

The anatomical separation of the M and P pathways begins at the level of the retinal ganglion cells where two groups of cells exist: the M and P cells. M cells give transient responses to stimulus onset and offset, have large receptive fields and rapidly conducting axons. These properties differ from P cells that respond in a more sustained fashion, have smaller receptive fields, and have axons that conduct more slowly. (Lennie, Trevarthen, Van Essen & Wassle, 1990; Schiller, 1986). M-cells are broad-band cells

with high contrast sensitivity while P cells are mostly colour-opponent cells with lower contrast sensitivity (DeYoe & Van Essen, 1988; Schiller, 1986). The retinal ganglion cells project to the six laminae of the lateral geniculate nucleus (LGN), located in the thalamus. The M-cells project to the two most ventral laminae of the LGN and the P cells project to the four more dorsal laminae of the LGN (Schiller & Malpeli, 1978). The connections between the two classes of retinal ganglion cells and the respective layers to which they project in the LGN is very well established (Leventhal, Rodieck & Dreher, 1981). The neurons in the LGN have properties almost indistinguishable from those of the ganglion cell inputs (Crook, Lee, Tigwell & Valberg, 1987; Lee, Valberg, Tigwell & Tryti, 1987).

When comparing M and P cells in the LGN in terms of sensitivity to temporal frequency, a major difference is quite apparent. Both cell types respond to gratings moving between 10 and 20Hz, but the sensitivity of the M cells is band-pass with peak sensitivities at higher temporal frequencies and a fairly rapid decline in sensitivity at lower temporal frequencies. This differs from the sensitivity of P cells that show a low-pass temporal-frequency response and a rapid loss of sensitivity at high temporal frequencies (Derrington & Lennie, 1984). Neither group of cells within the LGN is directionally selective (Van Essen & De Yoe, 1995). When the spatial frequency of the moving grating is varied, M cells show substantially greater contrast sensitivity than P

cells to low spatial frequencies, while P cells have greater sensitivity than M cells to high spatial frequencies (Derrington & Lennie, 1984).

Anatomical and Physiological Properties of the Cortical Visual Pathways

Due to the cross-talk between the M and P pathways from V1 and onward (Van Essen & DeYoe, 1995), I will use these terms loosely when discussing the cortical areas. Nevertheless, cells from the M and P layers of the LGN project to different areas of layer 4 of the striate cortex (V1). As shown in Figure 1, the M-layer neurons project to 4Cα, which then projects to layer 4B. The P-layer neurons of the LGN project to layer 4Cβ. Organization within cortical area V1 becomes apparent when layers 2 and 3 are stained for cytochrome oxidase (CO) (DeYoe & Van Essen, 1988). There is an organization of CO-rich "blobs" separated by CO-sparse "interblobs". The "blobs" receive their input from both layer 4Cβ of the P pathway and layers 4Cα and 4B of the M pathway, while the "interblobs" receive their input from layer 4Cβ of the P pathway (Van Essen & DeYoe, 1995).

Staining for CO within V2 shows that this area is subdivided into alternating "thick" and "thin" stripes, both rich in CO, which are separated by CO-sparse "interstripes". The thick stripes receive their input from layer 4B of V1, while the thin

stripes and interstripes receive their input from the blobs and interblobs of V1, respectively.

In the M pathway, both layer 4B of V1 and the thick stripes of V2 project directly to extra striate area V5/MT. In the P pathway both the thin stripes and the interstripes project to extra striate area V4 (DeYoe & Van Essen, 1988). Area V4 of the P pathway projects onwards to inferotemporal cortex, while area V5/MT projects to the parietal areas (DeYoe & Van Essen, 1988). These areas include the ventral intraparietal area (VIP), medial superior temporal area (MST), lateral intraparietal area (LIP) and the posterior parietal cortex (PPC).

Within the aforementioned visual pathways, the cells in layer 4B are where many cells first show selectivity for movement direction. (Livingston & Hubel, 1987; DeYoe & Van Essen, 1988). In V2, cells within the thick stripes also have direction sensitivity. (Shipp & Zeki, 2002) but their receptive fields, like those in V1, are too small for motion integration across space (Lennie, Trevarthen, Van Essen & Wassle, 1990). With neurons in V5/MT having significantly larger receptive fields than those in V1 and V2 (Lennie et al., 1990), they are better suited for the analysis of global motion stimuli than direction-selective cells in other cortical areas (Schenk & Zihl, 1997). Global motion integration therefore becomes possible in cortical area V5/MT (DeYoe and Van Essen, 1988; Livingston & Hubel, 1987; Maunsell, & Van Essen, 1983).

Effects of Lesioning Subcortical Areas of the P Pathway

Lesion studies using monkeys can easily be related, a posteriori, to the known anatomy and physiology of M and P pathway neurons (Merigan & Maunsell, 1993). Hence, these studies provide a nice link between performance on psychophysical tasks and the neural correlates that mediate this performance. Most lesion studies have been at the level of the LGN where the two pathways are anatomically separated into different laminae (Lennie et al., 1990). I will focus on primate data most relevant to human psychophysics.

A study by Merigan and Eskin (1986) used a neurotoxicant which killed most of the retinal ganglion cells that project to the parvocellular layers of the LGN, but spared the retinal input to the magnocellular layers. Spatio-temporal contrast sensitivity was measured with counterphase-modulated gratings in control monkeys and in monkeys treated with the neurotoxicant. The treated monkeys had substantially decreased contrast sensitivity at low temporal and high spatial frequencies. These same monkeys, however, had preserved function at high temporal and low spatial frequencies. In the same study Merigan and Eskin also examined flicker resolution thresholds to unpatterned sinusoidal flicker. Flicker thresholds were not affected by treatment with the neurotoxicant. These results are consistent with the proposal that the subcortical P pathway contributes to the

perception of low temporal and high spatial frequencies, but does not mediate the perception of high temporal and low spatial frequencies.

Merigan, Katz and Maunsell (1991) have similarly examined the effects of lesions to the P layers of the LGN. They measured monocular acuity and contrast sensitivity before and after a lesion to parvocellular layers 4 and 6 of the contralateral LGN. The display for both tasks consisted of either vertical or horizontal sinusoidal gratings and the task was to decide the grating orientation. Acuity was measured by finding the highest spatial frequency at which orientation discrimination was possible. The lesions caused a 3-to 4.5-fold decrease in visual acuity. Contrast sensitivity was measured by finding the lowest luminance contrast at which orientation of a stationary 1 c/deg grating was possible. Contrast sensitivity was severely reduced in monkeys with P-layer lesions, while no effect was found for a comparison monkey with a lesion to the M layers of the LGN. Collectively, the authors took these findings to support previous findings (Merigan & Eskin, 1986) that high spatial and low temporal frequencies are mediated through the subcortical P pathway.

Merigan, Katz, et al. (1991) also assessed chromatic contrast sensitivity to stationary isoluminant red-green gratings of 2 c/deg spatial frequency. A lesion to the P layers of the LGN caused a decrease in detecting chromatic contrast. This result

supported previous evidence that the P pathway is involved in colour contrast sensitivity (Merigan, 1989) and colour discrimination (Schiller, Logothetis & Charles, 1990).

Effects of Lesioning Subcortical Areas of the M Pathway

Lesions of the M pathway cause effects complementary to those caused by P pathway lesions. In a study by Merigan and Maunsell (1990) small lesions were placed in M layers of the LGN of monkeys. They assessed contrast sensitivity to various sinewave gratings. The lesion caused a decrease in sensitivity to stimuli of low spatial (1 c/deg) and moderate temporal (10Hz) frequency. The lesions did not affect sensitivity to a higher spatial frequency (2 c/deg) with no temporal modulation. The authors took these results to indicate that the contrast sensitivity to low spatial and moderate temporal frequencies depends on the integrity of the M pathway.

Merigan and Maunsell (1990) also examined the effect that this lesion had on maximum flicker resolution, which is also known as the critical flicker frequency (CFF). The lesion caused a profound decrease in CFF when modulation depth was low. When the modulation depth of flicker was 22% of the maximum luminance change possible, CFF decreased approximately 50%. This finding are consistent with the proposal that the subcortical M pathway plays an important role in flicker perception.

The effect of lesions to the M layers of the LGN on flicker detection has also been examined. Schiller et al. (1990) determined the effect of such a lesion on the detection of sinewave flicker at rates between 5 and 25 Hz. The results showed that there was no significant deficit in flicker detection in monkeys with P-layer lesions. Conversely, flicker detection at all temporal frequencies decreased as a result of the M-layer lesions. The mean luminance of the flicker was about 9 cd/m^2, with a variation of approximately 0.5 cd/m^2. Additionally, CFF was reduced to flicker rates between 11 and 17 Hz (Schiller et al., 1990). These findings further support the essential role of the subcortical M pathway in flicker perception.

A study by Maunsell, Nealy and DePriest (1990) examined cortical responses of neurons in area MT while blocking the responses of particular layers of the LGN and presenting flashing or moving stimuli within the receptive fields of MT neurons. Of the 57 MT sites tested, almost all sites had reduced responses when the magnocellular inputs were blocked. In fact, in most cases, responses were completely eliminated. Blocking the P pathway inputs, however, usually failed to produce a clear reduction in MT responses and rarely had a strong effect (Maunsell et al., 1990). These results show that the magnocellular layers of the LGN are the major contributors to responses in the V5/MT, in contrast to parvocellular layers, which provide a much smaller component.

Effects of Lesioning Cortical Area V5/MT

A study by Newsome and Pare (1988) examined the effect of a direct lesion of the monkey cortical area MT, where most neurons have selectivity for stimulus direction and speed (Maunsell & Van Essen, 1983). When tested in the hemifield contralateral to the lesion, thresholds were increased by 400 to 800%. However, thresholds measured simultaneously in the control hemifield were entirely within the range of pre-lesion performance. This shows that area MT plays a critical role in the perception of motion, specifically direction discrimination. This provides evidence of a clear link between performance on a psychophysical task of global motion perception and underlying physiology that mediates this performance. Subsequent MT lesion studies support the finding that area MT is essential for global motion perception (Rudolph & Pasternak, 1999).

Zihl, Von Cramon and Mai (1983) examined visual perception in a human patient, named LM, who had bilateral damage in an area likely to contain the human homologue of V5/MT. While LM had normal performance on most visual tasks, this patient had a severe motion perception deficit. This provided evidence that the human cortex contains an area that is functionally equivalent to area V5/MT found in monkeys. In a follow-up study on patient LM, Baker, Hess and Zihl (1991) showed that LM's performance on a global motion task decreased sharply, as compared with normal controls, when coherence

levels were decreased. Furthermore, they showed that in a task where non-moving noise dots were added, LM's performance significantly decreased with the addition of even a small percentage of dots, while normal controls were able to discriminate direction of the signal dots almost perfectly. Baker, Hess and Zihl (1991) took these results to indicate that LM's lesions cause a significant deficit in direction discrimination that results from impairment in processing stimuli with low signal-to-noise ratio. This finding is further supported by the results of Vaina, Alan and Cowey (1999), who measured motion coherence thresholds on a global motion task in a patient with a unilateral lesion in the vicinity of V5/MT. The global motion task was similar to that used by Newsome and Pare (1988). They showed that the patient had elevated motion coherence thresholds in the contralateral visual field.

Neuroimaging and Cortical Area V5/MT

Neuroimaging studies have provided support for a homolog of cortical area V5/MT in humans. Studies using positron emission tomography (PET) (Zeki, Watson, Lueck, Friston, Kennard & Frackowiak, 1991), magneto-encephalography (MEG) (Anderson, Holliday, Singh & Harding, 1996) and functional magnetic resonance imaging (fMRI) (Tootell et al, 1995) have shown that the location of human V5/MT is

near the occipito-temporal border in a minor sulcus immediately below the superior temporal sulcus.

Neuroimaging studies have shown that cortical area V5/MT has been shown to give a greater response to moving stimuli, as compared with stationary stimuli (Toottell et al., 1995; Zeki et al., 1991). Additionally, V5/MT is more active when viewing coherently moving dots of 5 and 20 deg/s than when viewing spatially and temporally comparable dynamic noise (Braddick, O'Brien, Wattam-Bell, Atkinson, Hartley & Turner, 2001). The latter authors took this result to further support the finding of studies comparing moving and stationary stimuli, by indicating that differences in activation do not simply reflect a high-temporal-frequency response. V5/MT has also been shown to have an increased activity during viewing of stationary stimuli preceded by an adaptation to a stimulus moving continuously in a single direction (Tootell et al., 1995). The authors took this result as physiological evidence that neurons in human cortical area V5/MT, like those in monkey V5/MT, are directionally selective.

Global Motion Perception in Clinical Populations

Global motion perception has been studied in several clinical populations. Coherence thresholds have been shown to be elevated in individuals with optic neuritis (Barton & Rizzo, 1994) and glaucoma (Silverman et al., 1990). Optic neuritis and

glaucoma are clinical conditions with known subcortical pathway damage, suggesting that normal human motion perception requires an intact subcortical M pathway.

The Shortcoming of Monkey and Human Subcortical M Pathway Lesion Studies

As previously mentioned, monkey lesion and human clinical studies have suggested that both the subcortical M pathway and cortical area MT are required for motion perception. The shortcoming of these studies is that the participants have brain damage and it is therefore not clear what to conclude about the role of the subcortical M pathway in normal motion perception. This was examined in the current study.

The current human psychophysical study was based on monkey single-cell physiology, a technique termed "psychoanatomy" (Blake, 1994). It was my goal to use two psychophysical techniques to support and expand on the results of lesion studies. These two techniques included: 1) adapting participants to full-field sinusoidal flicker prior to the presentation of stimuli, and 2) presenting stimuli on a red background. The development of these two techniques has arisen from knowledge regarding the underlying physiology of the monkey's M pathway. Thus, each technique will be reviewed in terms of how it affects subcortical M pathway physiology and then in terms of psychophysical studies that used it in conjunction with various perceptual tasks.

The Subcortical M pathway is Sensitive to Flicker

Two lines of physiological research have shown that the subcortical M pathway is needed for mediating flicker perception: single-cell recordings and lesion studies. In a study by Lee, Martin and Valberg (1989) the responses of macaque retinal ganglion cells to flicker were recorded. They found that M cells responded more vigorously to luminance flicker than P cells at temporal frequencies including 1, 2, 4, 10, 20 and 40 Hz. The greatest response of M cells (impulse/s) was shown to be at 10 Hz. The flicker sensitivity was similar in M cells with on and off centre receptive fields. The authors then compared these findings with contrast sensitivities to the same flicker frequencies of six humans. Subcortical M-cell sensitivity was found to be broadly similar to human sensitivity to flicker (Lee et al., 1989), showing that M cells are likely the neural correlate for flicker perception. The results of previously mentioned monkey lesion studies showed that a lesion to the M layers of the LGN resulted in decreased CFF (Merigan & Maunsell, 1990) and flicker detection (Schiller et al., 1990). This indicated that the subcortical M pathway is essential for flicker perception.

Flicker Adaptation Desensitizes the Subcortical M Pathway

Several studies have examined the effect that flicker adaptation has on visual perception. Two separate studies have shown that sensitivity to flicker decreased

following flicker adaptation (Nilsson, Richmond & Nelson, 1975; Pantle, 1971). This was measured by determining the modulation threshold for which participants could detect flicker in a test stimulus. While both of these studies showed that the most effective adapting frequency depended on the test frequency, Nilsson et al. (1975) showed that the effects of flicker adaptation tended to be fairly broad. Adaptation to a flicker frequency of 8 Hz decreased flicker sensitivity for all flicker frequencies between 4 and 24 Hz.

Green (1981) later showed that flicker adaptation decreased performance on a task that required detecting moving gratings. Green showed adaptation to 16 Hz flicker elevated contrast sensitivity thresholds for drifting or counterphase-flickering gratings with spatial frequencies between 0.5 and about 3-4 c/deg. Contrast sensitivity thresholds for higher spatial frequencies were not affected by flicker adaptation. Giaschi (1990) later confirmed that flicker adaptation to 8 Hz flicker raised contrast detection thresholds for drifting or counterphase-flickering gratings of spatial frequencies below 2 c/deg. The spatial and temporal tuning of these results suggest that flicker adaptation disrupts the functioning of the M pathway, most likely at the subcortical level. The effect of flicker adaptation on global motion perception, which requires integrating motion signals across a large portion of the visual field, has not yet been examined. This was examined in the current study.

Subcortical M-Pathway Functioning is Disrupted by Red Light

Most M cells have broadband wavelength sensitivity (Schiller et al., 1990), but a subclass of cells within the subcortical M pathway is sensitive to long wavelengths of light. Weisel and Hubel (1966) were the first to find this subclass of cells, which they named Type IV neurons, in the M layers of the monkey LGN. These neurons have a center-surround mechanism where the center and surround have different spectral sensitivities. With an inhibitory surround that is selectively sensitive to long wavelengths of light (De Monasterio & Schein, 1980; Dreher et al., 1976; Kruger, 1977; Lee, 1996; Livingstone & Hubel, 1987; Shapley, 1990; Weisel & Hubel, 1966), these neurons are considered to have colour opponency (De Monasterio & Schein, 1980). Both the phasic-type responses of these neurons and their normal spontaneous activity are suppressed in the presence of a large red field (Dreher et al., 1976; Kruger, 1977; Weisel & Hubel, 1966). At the level of the retina, these neurons are more frequently encountered in the foveal region (De Monasterio, 1978) and likely arise from a spatial imbalance of cone inputs between the centre and surround regions, with the surround receiving stronger long (L)-cone input (De Monasterio & Schein, 1980; Reid & Shapley, 1992). The discovery of type IV neurons and their physiological properties led to psychophysical experiments designed, discussed hereafter, to assess the effect of these neurons on perception.

A Red Background Changes Visual Perception

Breitmeyer and Williams (1990) were the first to assess the effect of a red background on task performance. They used a task of metacontrast masking in which the presentation of a target is followed by the presentation of a mask which suppresses the perception of the target at specific temporal separations (Alpern, 1953). According to the model of metacontrast masking put forward by Breitmeyer and Ganz (1976), both the target and the mask cause quick activation of the M system followed by a longer response by the P system. Suppression of the target by the mask is hypothesized to result from the mask's quick M system response, which inhibits the P system's slow response elicited by the target. Hence it is thought that the magnitude of metacontrast masking may be used to assess the strength of M system response; greater metacontrast masking implies a stronger M system response. The presence of a diffuse red background in metacontrast experiments has been shown to decrease the magnitude of metacontrast masking (Breitmeyer & Williams, 1990; Edwards, Hogben, Clark & Pratt, 1996; Pammer & Lovegrove, 2001). A red background has also been shown to decrease the subjective apparent motion in a stroboscopic motion display (Breitmeyer & Williams, 1990). A Ternus display consists of the successive presentation of two overlapping frames, each consisting of three equidistant and horizontally arrayed elements. The only difference between frame 1 and frame 2 is that the second frame's three elements have all been

moved by one element to the right. Thus, when presented in succession the first frame's central and right element are aligned with the second frame's left and central elements. A study by Slaughuis, Twell and Kingstone (1996) found that a red background decreased group motion perception of a Ternus display (perception of all three elements moving to the right). This effect of a red background on the perception of movement in a Ternus display was not, however, replicable in another study (Pammer & Lovegrove, 2001).

Most of these psychophysical findings have speculated that a red background decreases the functioning of the M pathway. For all the tasks that have been used, however, there is no physiological evidence suggesting that the M pathway specifically mediates performance. The effect of a red background on human global motion perception has not yet been examined. This was examined in the current study.

Predictions of the Current Study

The two psychophysical techniques used in this study were flicker adaptation and the presence of a red background. Assuming that the subcortical M pathway is part of the neural correlate needed for global motion perception, I predict that both techniques will result in elevated coherence thresholds. Based on M pathway physiology, I further predict that the red background will produce less threshold elevation than flicker adaptation. This prediction is based on the fact that although type IV neurons are tonically suppressed in

the presence of red light, studies have shown that these neurons comprise approximately 11 % (Dreher et al., 1976) or 15% (Weisel & Hubel, 1966) of the neurons in the M pathway. It has been suggested that these figures may be underrepresented, however, if type IV cells represent extreme examples in foveal spectral changes rather than a separate subgroup of cells within the M pathway (De Monasterio & Schein, 1980). Nevertheless, I assume that a red background will not disrupt as many neurons in the M pathway as compared with flicker adaptation. Since maximal sensitivity of subcortical M neurons has been shown to be at 10 Hz (Lee, et al., 1989) and the effects of flicker adaptation appear to be quite broad (Nilsson et al., 1975), most M neurons should be affected when adapted to 10 Hz flicker.

Methods

Participants

Thirty individuals (12 men and 18 women, mean age = 23.6, range of age = 18 to 40 years) participated in this experiment. Most of the participants were undergraduate students who received course credit for participation. All participants had normal or corrected-to-normal visual acuity and normal colour vision.

Apparatus

The participant's visual acuities was measured using the Regan 96% contrast letter chart (Regan, 1998). Colour vision was assessed using Farnsworth's D 15 test. Custom Matlab code was used to generate stimuli on a Macintosh G4 computer and display them on a 17″ Macintosh monitor with a resolution of 1024 x 768 pixels (width x height). The monitor refresh rate was 75 Hz.

Design and Procedure

A run began with a fixation cross that appeared in the center of the screen 20 x 27 deg (height x width). The fixation cross remained on the screen until the global motion stimuli appeared. The stimuli for the global motion task consisted of white dots that were 0.1 deg in diameter. The dot density was 1.0 dot/deg^2 and dots always moved at a constant speed of 0.935 deg/s. Stimuli were presented for a total of 4 frames, each frame lasting 4 screen refreshes. The duration of each trial was therefore 213 ms. Dots had a limited lifetime, meaning that while the proportion of dots that carried the motion signal remained constant on a given trial, the actual dots carrying the motion signal were randomly reselected at the beginning of each frame. Therefore, participants could not discriminate the direction of motion by simply following the trajectory of a single dot. Within a run, a new trial began every 5 s. In between presentations of stimuli, the fixation

cross re-appeared in the center of the screen. In each run stimuli were presented in a 2-down-1-up staircase fashion, beginning with 100% coherence. This means that the participant had to answer correctly twice at a given coherence level before the coherence level was decreased. Every time the participant made an error the coherence level was automatically increased. The first step size was at increments of 20% coherence. This means that after answering correctly twice on the first two trials of the experiment, the coherence level decreased from 100% to 80% coherence. Each time the coherence level changed direction (i.e., from decreasing to increasing, or vice versa) was considered a reversal. From the third reversal onward, the step size was halved at each reversal until reaching the minimum step size of 1% coherence. A block ended when 10 reversals were obtained. The experiment consisted of four runs: two experimental conditions, each with its own control condition.

The first experimental condition began with flicker adaptation, while its control condition began with adaptation to a gray field. The initial adaptation period was two minutes in length. In the flicker adaptation condition, participants adapted to full-field sinusoidal flicker with a frequency of 9.375 Hz. The minimum and maximum luminance of the flickering field was 1 and 100 cd/m^2, respectively, providing a mean luminance of 50.5 cd/m^2. The mean luminance of the gray field in the control condition was 50 cd/m^2. The mean luminance of the monitor remained at this level throughout a run for both

conditions. Five seconds before the end of the adaptation phase, the computer presented four descending tones to indicate the beginning of the motion trials. In both of these conditions a re-adaptation period of 387 ms was presented between the motion trials.

The second experimental condition consisted of presenting the motion trials on a red background, while its control condition consisted of presenting stimuli on a gray background. Each condition began with the presentation of a red or gray field, respectively. The first stimulus was presented only 5 s after the field appeared because neither of these conditions involved adaptation. Both the red field and the gray field became the respective background colour when the moving white-dot stimuli were presented. The screen returned to the uniform red or gray field for 387 ms between motion trials. The red colour of the experimental condition had a mean luminance of 30 cd/m^2. The gray background in the control condition also had a mean luminance of 30 cd/m^2. The mean luminance of the monitor remained at this level throughout a run for both conditions.

The experiment was conducted in a dimly lit room and no head restraint was used. Stimuli were viewed binocularly at a viewing distance of 74 cm. Prior to beginning each run, the viewing distance was measured and the participant's sitting location was adjusted accordingly.

Prior to beginning the experiment a practice session was completed, in which participants completed 4 runs of 20 trials in a similar staircase fashion as described above. The stimuli were white dots on a gray background with a mean luminance of 50 cd/m^2. Participants then completed the experimental session, which consisted of one run of each of the two experimental conditions and their respective control conditions. The order of these four conditions (ABCD, BCDA, CDAB, & DABC) was counterbalanced across participants to control for sequence effects (Winer, Brown & Michels, 1991). Participants were given a 'game pad' for which two buttons were used to enter their responses. They were instructed to press the button on the left if they perceived most of the motion to be leftward, to press the button on the right if they perceived most of the motion to be rightward and to guess when unsure. They were instructed to respond as quickly and accurately as possible once the dots had left the screen on each trial. This ensured responses were recorded prior to the next stimulus being presented. Each run provided a threshold measure of motion coherence. This threshold indicates the minimum proportion of dots that must be moving coherently in the same direction in order for the participant to accurately discriminate the direction of motion. Thresholds were determined by fitting Weibull functions (Watson, 1979) to the psychometric functions for each participant. The threshold was defined as the point at which 82% of the responses were correct.

Results

For each of the four conditions motion coherence thresholds were averaged across all participants. Figure 2 shows average coherence thresholds for each condition.

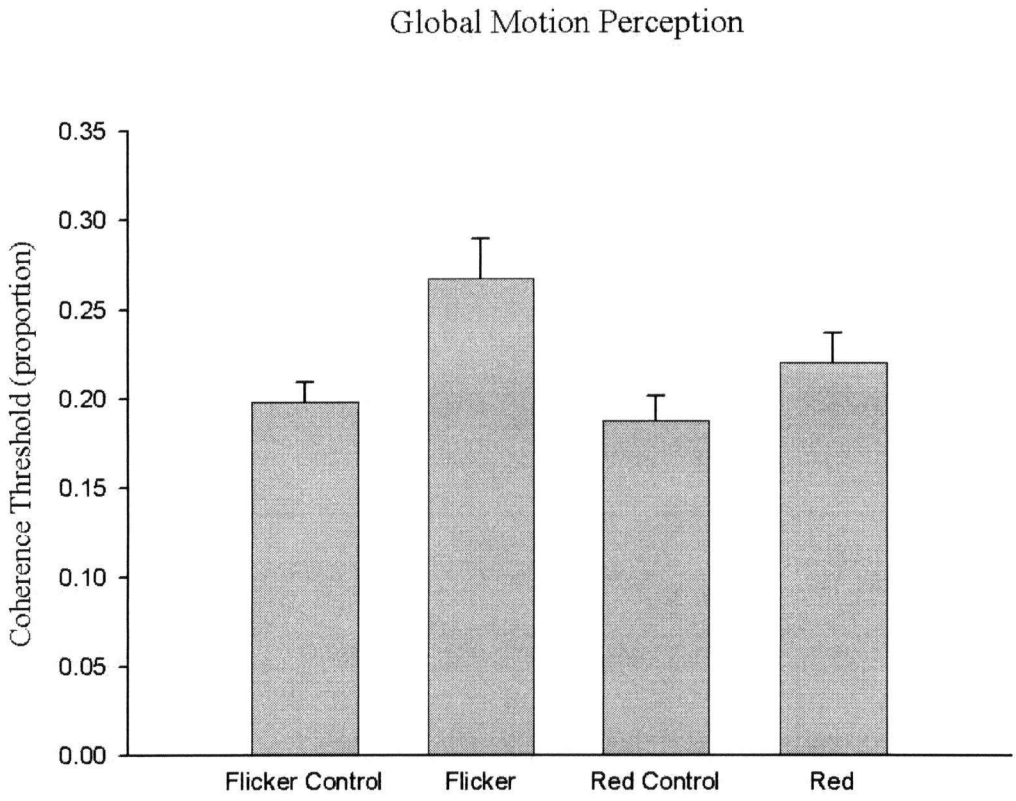

Figure 2. Coherence thresholds for direction discrimination with and without adaptation to a 9 Hz flickering field or the presence of a red background.

The mean coherence threshold in the flicker control condition was lower (M = 0.1981, SD = 0.0598) than the mean coherence threshold in the flicker adaptation condition (M = 0.2671, SD = 0.1217). Figure 2 also shows that the mean coherence threshold of the red control condition was lower (M = 0.1873, SD = 0.0776) than the mean coherence threshold of the red background condition (M = 0.2198, SD = 0.0954). A planned orthogonal contrast showed that the difference in coherence thresholds between the flicker control and flicker adaptation conditions was significant ($F_{1,126} = 18.34$; $p < 0.001$). This result shows that global motion perception was worse when participants had been adapted to full-field sinusoidal flicker. A second planned orthogonal contrast showed that the difference in coherence thresholds between the red control and red background condition was significant ($F_{1,126} = 4.07$; $p < 0.05$). This result shows that global motion perception was worse when participants had stimuli presented on a red background as opposed to a gray background. A third planned orthogonal contrast comparing the threshold elevation that resulted from flicker adaptation or the red background indicated a significant difference ($F_{1,126} = 6.05$; $p < 0.025$). This indicates that adaptation to full-field sinusoidal flicker increased motion coherence thresholds by a greater magnitude than that caused by presenting the stimuli on a red background.

Figure 3 compares the threshold elevation on the global motion task that resulted from flicker adaptation vs. a red background. Each data point represents the threshold

elevation in a participant's coherence threshold for both experimental conditions, as compared with their respective control conditions. This value was calculated by subtracting a participant's coherence threshold in the control condition from that of the experimental condition, dividing this value by the coherence threshold of the control condition and then multiplying this value by 100%.

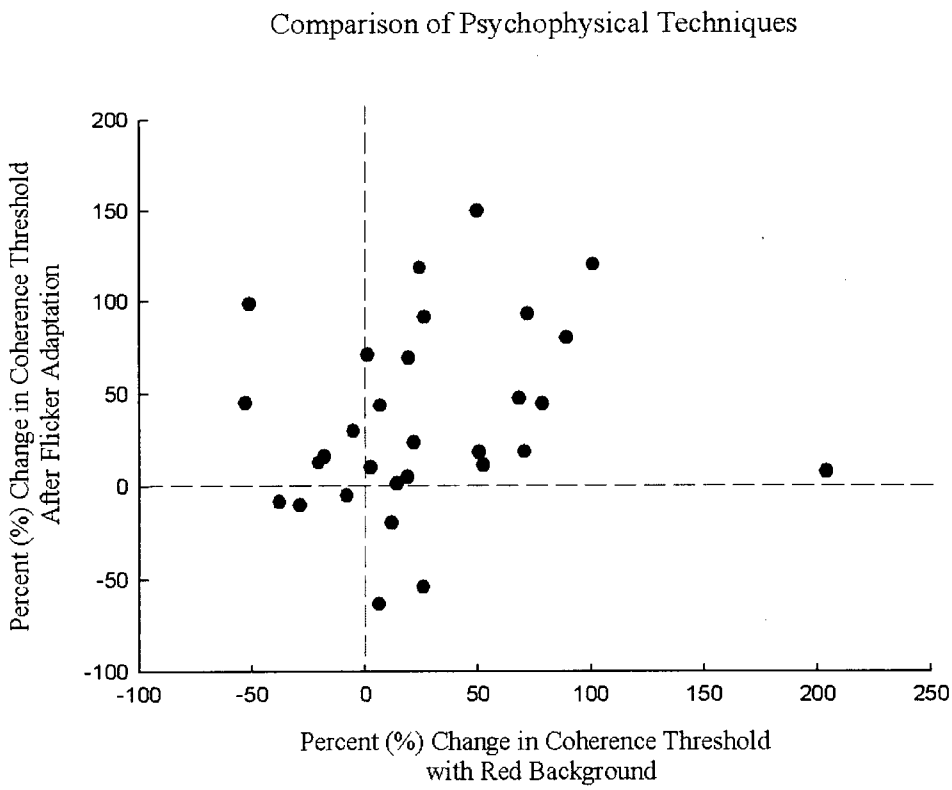

Figure 3. Percentage change in coherence thresholds for direction discrimination after flicker adaptation vs. in the presence of a red background.

From Figure 3 we notice that 27 of the 30 participants showed elevated coherence thresholds on at least one task. Of these 27 participants, 19 had thresholds that increased in both experimental conditions. Five participants had increased thresholds as a result of only flicker adaptation, while three participants had increased thresholds as a result of only the red background. Flicker adaptation raised coherence thresholds by an average of 34.8%, while the presence of a red background raised coherence thresholds by an average of 17.4%.

Discussion

Two psychophysical techniques included in this study were adaptation to full-field sinusoidal flicker and presenting stimuli on a red background. Given the physiological properties of the subcortical M pathway in monkeys, one would predict that these techniques would temporarily disrupt normal functioning of this part of the pathway. When each of these techniques was used in conjunction with a global motion task, motion coherence thresholds were elevated. In fact, the results shown in Figure 3 indicate that the majority of participants showed elevated coherence thresholds in both experimental conditions. This indicates that both techniques were quite capable of disrupting subcortical M-pathway functioning, thereby causing poorer performance.

I predicted that the two psychophysical techniques used should differ in their ability to disrupt M-pathway functioning. This prediction was based on the physiological properties of the M pathway (Dreher et al., 1976; Lee et al., 1989; Weisel & Hubel, 1966). Since flicker adaptation likely affects most cells in the M pathway, while a red background only affects a certain proportion of cells, I predicted that flicker adaptation should be more disruptive on M-pathway functioning. Indeed, flicker adaptation decreased performance on the global motion task by a significantly greater magnitude than was caused by the red background. This finding shows a clear relationship between what likely happens at a physiological level and behaviour or perception. Additionally, this finding demonstrates that flicker adaptation is the more powerful technique to be used in future studies where temporarily disrupting normal M-pathway functioning is desired. This might include attempting to determine what aspects of reading or attention the subcortical M pathway may facilitate.

In a manner parallel to monkey lesion studies, I used a non-invasive psychophysical technique to show that a disruption to the magnocellular pathway decreases motion perception. It is interesting to consider this in the context that there is much agreement that cortical area MT is the main motion-processing center of the brain and that this is where global motion integration becomes possible (DeYoe and Van Essen, 1988; Livingston & Hubel, 1987; Maunsell & Van Essen, 1983). There is no

known physiological evidence suggesting that flicker adaptation or a red background would disrupt the M pathway beyond the level of the M layers of the LGN. While there is no physiological evidence that neurons in the M layers of the LGN respond with greater sensitivity to movement or have directional sensitivity, my results show that when the functioning of the subcortical human M pathway is disrupted, there is a decreased ability to perceive global motion. It is therefore likely that neurons at this level of the visual pathway are in fact carrying local motion information that is essential for higher cortical processing.

As previously mentioned, some clinical populations have elevated coherence thresholds on global motion tasks. While the stimuli across these studies were not identical, it is interesting to compare these results with the present findings. First of all, this is the first study to show that inducing a disruption of the human subcortical M-pathway affects global motion perception. Secondly, in previously mentioned studies, one clinical groups had an average coherence threshold elevation of 70% (Silverman et al., 1990). The current study showed that flicker adaptation raised coherence thresholds by an average of 34.8%, while a red background raised coherence thresholds by an average of 17.4%. This comparison shows that flicker adaptation is not as effective in elevating coherence thresholds as actual functional pathology.

The motion pathway I have described is the geniculostriate pathway. This pathway projects to the LGN and then to cortical area V1 before projecting onward to V5/MT. There is evidence that this is a pathway for carrying slow visual motion information and that another less prominent motion pathway carries fast visual motion information (ffytche, Guy & Zeki, 1995). This less prominent motion pathway is called the tectopulvinar pathway. At the level of the retinal ganglion cells, the tectopulvinar pathway projects to the superior colliculus, which then projects to its thalamic target, the pulvinar. The pulvinar consists of lateral, inferior and medial divisions, all of which project onward to cortical area MT (Standage & Benevento, 1983). While little research has examined the role of this pathway in motion perception compared with the massive pathway that reaches V5 through V1, there is no reason to suppose that it has no function (ffytche, et al. 1995).

A study by Rodman, Gross and Albright (1989) has shown that there is considerable conservation of V5/MT response properties after removal or inactivation of visual area V1 in primates. The remaining responsive cells respond in a directionally selective manner comparable to that seen in normal V5/MT. These authors speculated that perhaps this residual responsiveness in V5/MT after removal of V1 was due to other subcortical routes by which visual information might reach V5/MT. The route suggested involved the superior colliculus and its thalamic target, the pulvinar. This was supported

in another study, which found destroying the superior colliculus after the V1 lesions totally eliminated the residual responsiveness originally found in V5/MT (Rodman, Gross & Albright, 1986).

Evidence for the functional significance of this pathway in humans comes from a positron emission tomography (PET) study that examined whether visual signals reach visual area V5 in a patient 'blinded' in one field by an extensive unilateral lesion of V1 (Barbur, Watson, Frackowiak & Zeki, 1993). The participant in this study was a 26 year-old patient, G. Y., who had sustained his injuries in a car accident at the age of 7 years. This left him with massive damage to the occipital lobe in his left hemisphere. G.Y. completed a motion direction discrimination task where a vertical bar was presented in the blind hemifield. The stimulus either moved at randomly selected speeds toward or away from a meridian, or remained completely stationary. G.Y.'s correct responses, pooled over all the PET scans, were 49% and 99% for the stationary and moving stimuli, respectively (chance = 50%). The PET scans indicated that indeed there was heightened activation in area V5/MT in the presence of moving stimuli (Barbur et al., 1993). It was noted that when stimulated with a moving stimulus, G.Y. verbally reported seeing movement. The authors took these results to indicate that visual motion information can reach area V5/MT through the tectopulvinar pathway, and that this information is sufficient for both the discrimination and conscious awareness of a visual stimulus.

There is also evidence that the tectopulvinar pathway carries motion information in normal adults. Using a technique that couples electroencephalograpy (EEG) with magnetoencephalograpy (MEG), ffytche et al. (1995) examined the timing of arrival of visual signals linked to motion in the visual cortex and of the sequence in which the various visual areas were activated. The stimulus consisted of a stationary checkboard. To elicit a movement response, the stationary phase was followed by coherent motion in one direction at speeds between 5 deg/s and 22 deg/s. The results of this study showed that signals reached V5/MT before area V1, when the visual motion was fast (22 deg/s). Conversely, signals to slow motion (<6 deg/s) arrived in V1 before reaching V5/MT. The authors took these results to indicate that activation of the tectopulvinar pathway is velocity dependent and becomes increasing active as stimuli move in excess of 6 deg/s. Pilot data I collected supported that the psychophysical techniques affected information carried by the slow pathway.

Two individuals in our laboratory, including the present author, participated in a pilot study. The stimuli were exactly the same as the current study, except now the dots moved at a faster speed of 8 deg/s, as compared with 1 deg/s. The two participants completed each of the two experimental and control conditions three times. The mean coherence threshold in the flicker control condition was ($\underline{M}$ = 0.0723, $\underline{SD}$ = 0.0332), the same as the mean coherence threshold in the flicker adaptation condition ($\underline{M}$ = 0.0750,

SD = 0.0651). Similarly, the mean coherence threshold of the red control condition was the same (M = 0.0957, SD = 0.0292) as the mean coherence thresholds of the red background condition (M = 0.0931, SD = 0.0295).

Based on the physiological properties of the subcortical M-pathway, a disruption of its normal functioning likely results from the two psychophysical techniques used in the current study. This disruption did not affect coherence thresholds for the faster motion used in the pilot study. It is therefore possible that the motion information for the faster stimulus relied on the pathway through the parallel tectopulvinar pathway, which has been shown to carry fast motion information (ffytche et al., 1995). With the subcortical M pathway disrupted, it appears that the stimulus was sufficiently fast to activate the tectopulvinar pathway and avoid any changes in coherence thresholds. The psychophysical techniques used in the current study elevated coherence thresholds on a global motion task with slower motion. This supports that the effects of the psychophysical techniques were on the geniculostriate pathway. These results might help us understand the neural mechanisms underlying deficits in motion perception. For example, a deficit in slow motion perception may be indicative of a problem with the motion pathway that projects to the LGN and V1 prior to projecting to V5/MT, while a deficit in fast motion perception may be indicative of a problem with the tectopulvinar pathway.

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Appendix

One-Between Four-Within repeated measures ANOVA (simple effects)

Motion coherence thresholds

Source	SS	DF	MS	F	P
disruption techniques	0.113	3	3.754 e-02	9.645	<0.001
error	0.339	87	3.893e-03		