

CYCLOPEAN MOTION AFTEREFFECTS USING SPIRAL PATTERNS:
DISSOCIATION BETWEEN LOCAL AND GLOBAL PROCESSING

By

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Abstract

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The cyclopean motion aftereffect refers to the illusory perception of motion in one direction evoked by the selective adaptation to real motion of disparity (binocular depth) information in the opposite direction. Employing a paradigm created by Cavanagh and Favreau (1980), this study induced cyclopean motion aftereffects using a standard-image log spiral as an adapting pattern, and a standard-image or a mirror-image log spiral as a test pattern, with the latter used to cancel local motion mechanisms. Our results reveal that the durations for both the cyclopean and luminance motion aftereffects declined when a mirror-image test pattern was used relative to when a standard-image test pattern was used. This indicates that there are two levels of cyclopean motion processing, local versus global, and that these levels are analogous to those found in luminance motion processing.

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Figure 2. Mean MAE duration for the standard-image and mirror-image test patterns, for cyclopean and luminance stimuli. Each data point is the mean of 10 observers. Each error bar represents \pm one standard error of the mean.

CHAPTER ONE

INTRODUCTION

As we move through the world, each eye receives a slightly different view, which is due to the horizontal separation between the eyes. This slight difference between the two eyes views is called binocular disparity. Normally the two disparate views are fused together, in the brain, thereby creating a binocular cue about the relative depth of objects in the environment (Howard, 2002; Howard & Rogers, 2002; Patterson & Martin, 1992). Because the two eyes' views are processed at binocular-integration levels of the visual system, the perception of binocular depth is sometimes called cyclopean perception to reflect the fact that binocular integration occurs at a central site in the visual cortex (Julesz, 1971).

Movement through our world, and interaction with objects that exist in physical space, will result in lateral shifts of the retinal images and therefore produces dynamic variation in the available disparity information. Dynamic variation in disparity is one of the cues for perceiving the trajectory of objects moving in depth, which is the result of disparity change computed as a time function (Cavanagh & Mather, 1989; Patterson 1999; Regan 1993). As the binocular disparity shifts over time, a vector is defined for a motion path through space.

The processing of cyclopean motion has a number of interesting characteristics. As one example, the cyclopean system uses coarse spatial information for the processing of motion in depth. The low spatial resolution results in poor object detection. Thus, this system cannot be used for detection of small objects or to distinguish fine details in an

object; only the detection of the presence and the motion path of larger, more coarse objects in the environment can be obtained (Tyler, 1974). As another example, the cyclopean system uses coarse temporal information as well. That is, this system is a sluggish system which results in poor temporal resolution (Patterson, Ricker, McGary & Rose, 1992).

Cyclopean motion processing has another interesting characteristic in that it is directionally selective. Phinney, Bowd and Patterson (1997) found that mechanisms that detect cyclopean motion have directional selectivity, with the angular distance between neighboring mechanisms being approximately 20 to 30 degrees. The directional tuning is suggestive of a distributed-channel neural-coding scheme. Under such a scheme, neural-coding of direction is achieved through a pooling of responses of cells that have different preferred directions of tuning. (Levinson & Sekuler, 1976; Mather & Moulden, 1980).

Given that cyclopean motion processing has the properties detailed above, it is interesting to consider whether this processing takes place across different stages of the motion stream. Interestingly, the levels of processing of cyclopean motion are currently being debated via two competing theoretical frameworks.

In the first framework, Lu and Sperling (1995, 2001) posit that there exist three levels of processing in the motion stream. The first level of processing, called first-order motion processing, involves detecting the movement of luminance-defined boundaries. This type of motion-sensing system, defined by Adelson and Bergen (1985), uses a basic motion energy computation involving frequency filtering of luminance information followed by squaring and pooling operations. The second level of processing, called second-order motion processing, entails detecting the movement of contrast-defined or

texture-defined boundaries. Second-order motion-detecting mechanisms process moving stimuli via the operation of front-end filtering (signal rectification) which is followed by a motion-energy computation (Cavanagh & Mather, 1989). The third level of processing, called third-order motion processing, detects the movement of object boundaries that appear strongly as figure against ground, such as chromatic boundaries and, importantly, cyclopean depth boundaries. A controversial proposal by Lu and Sperling (1995, 2001) is that the operation of this third-order motion system is based on an attentionally-modulated “saliency map.” This system uses spatiotemporal changes in the saliency map as an input to a high-level motion-energy computation. As a key component in this framework, visual attention serves to amplify or attenuate signals based upon the saliency of the moving object.

Importantly, Lu and Sperling (1995, 2001) argue that third-order motion processing occurs at a high level of the motion stream where motion information is globally pooled from lower-level (local) motion detectors. On this idea, there is physiological evidence (e.g., Movshon, Adelson, Gizzi & Newsome 1985; Newsome & Paré, 1988) and psychophysical evidence (e.g., Cavanagh & Mather, 1989) that signals from lower-level motion detectors are pooled at higher levels of the motion stream, such as in area MT. Such pooling occurs within and across the different motion pathways. It is at this level of global motion pooling where Lu and Sperling posit that third-order cyclopean motion processing occurs.

In the second framework, Patterson (1999, 2002) proposes that there exists two levels of processing in the motion pathway, first-order and second-order, which are analogous to the first two processing levels of Lu and Sperling (1995, 2001) outlined

above. However, in Patterson's framework, cyclopean motion is processed by a second-order system, rather than a third-order system, via front-end disparity detection followed by a motion-energy computation applied to the disparity domain. This processing is accomplished through the operation of relatively lower-level mechanisms which do not rely on visual attention or feature tracking as posited by Lu and Sperling (1995, 2001). Support for this framework was reported by Patterson, Fournier, Wiedeger, Vavrek, Becker-Dippman and Bickler (2005), who found that diverted attention did not impact the generation of the cyclopean motion aftereffect any more than it impacted a first-order (luminance) motion aftereffect, which suggested that cyclopean motion processing is not uniquely dependent upon visual attention.

The purpose of the present study is to investigate whether cyclopean motion is processed only at levels of the motion stream where motion signals are globally pooled, or whether it is processed at lower levels where local signals are generated, as well as at global levels. To do so, a spiral motion aftereffect paradigm was employed. The motion aftereffect (MAE) refers to the illusion of motion, of a static test pattern, in one direction following prolonged exposure (adaptation) to real motion in the opposite direction. This perception of illusory motion is thought to arise from the disruption of the equilibrium of activity in networks of cells that signal different directions of motion. Because the networks have been shifted away from equilibrium, the sudden removal of the adapting pattern of motion and replacement with a stationary test pattern results in a perception of the test pattern moving in the opposite direction (van de Grind, van der Smagt & Verstraten, 2004). Furthermore, it is likely that MAEs result from adaptation at multiple levels of motion processing, both local and global (Cavanagh & Favreau, 1980).

For example, consider the MAE paradigm developed by Cavanagh and Favreau (1980). Their paradigm dissociates MAEs derived from the adaptation of local, lower-level motion mechanisms from adaptation of global, higher-level motion mechanisms. This is done through the use of a spatial pattern configured as a spiral, for both the adapting and test patterns. Specifically, the spiral pattern follows a specific exponential function: $r=e^\theta$, where r is the radius and θ represents the angle at the origin in radians (giving the amount of rotation). When this type of spiral pattern is created, it follows an arc whose radius increases according to this exponential function.

Such spirals have a unique geometric property in that their mirror-image will create 90-degree angles at each and every intersection when superimposed on the original pattern. Thus, if MAEs are produced via the activation of different levels of motion processing, then the use of a spiral test pattern which is a mirror-image of the spiral adapting pattern should cancel the contribution of local motion mechanisms, leaving only the activity of global motion mechanisms. (The logic of this paradigm is based on the principle that local motion detectors are cancelled when elongated stimuli are imaged on receptive fields whose preferred orientation is orthogonal to the orientation of the stimuli.)

Employing first-order luminance stimuli, Cavanagh and Favreau (1980) found that when a spiral pattern was used as the adapting stimulus and its mirror-image was used as the test stimulus, the duration of the MAE was significantly reduced relative to when a non-mirror-image (standard-image) test pattern was employed. Presumably the local level of motion processing generates longer MAEs than the global level. Thus, the use of a mirror-image test pattern, reveals the contribution of only the global level of

motion processing, which elicits a shorter MAE than the standard-image test pattern which reveals the contribution of both local and global levels of processing.

The use of spiral patterns to generate MAEs provides a test of one aspect of the Lu and Sperling framework concerning third-order motion processing, namely its global nature. Recall that Lu and Sperling (1995, 2001) posit that cyclopean motion is processed only by a third-order system possessing global properties. This means that the duration of the cyclopean MAE should be similar when either a mirror-image or standard-image spiral is used as a test pattern because only global motion mechanisms should be involved in either case. If, however, the use of a mirror-image pattern for testing elicits a shorter cyclopean MAE than a standard-image pattern (analogous to the luminance MAE), then that would suggest that local motion mechanisms are contributing to the production of the cyclopean MAE in the latter case.¹ Note that it is reasonable to test for the effects of type of test pattern on cyclopean MAEs because there is abundant research showing that moving cyclopean patterns can induce robust MAEs (Bowd, Rose, Phinney and Patterson, 1996; Patterson & Becker, 1996; Patterson, Bowd, Phinney, Pohndorf, Barton-

¹ For cyclopean MAEs, it may be that the global level of processing generates longer MAEs than the local level. In this case, the mirror-image test pattern, which reveals the contribution of only global motion mechanisms, would elicit an MAE equivalent to the MAE elicited by the non-mirror-image test pattern because the contribution of the local motion mechanisms in the latter case would be overshadowed by the longer-duration global mechanisms. Thus, if the duration of the cyclopean MAE is similar when either a mirror-image or standard-image spiral is used as the test pattern, then an alternative interpretation is that both local and global motion mechanisms are involved in cyclopean motion processing but the global mechanisms generate longer MAEs. This interpretation would be one that supports a weaker version of the Lu and Sperling hypothesis, namely that cyclopean motion is processed at levels of the motion stream that emphasize global pooling operations.

Howard & Angilletta, 1994; Patterson et al., 2005). Luminance MAEs were generated for comparison to the cyclopean MAEs.

Thus, when both cyclopean and luminance stimuli are combined within the spiral MAE paradigm, the Lu and Sperling framework would predict an interaction between stimulus type and test pattern type: when going from the standard-image test pattern to the mirror-image test pattern, the luminance MAE should decline (replicating Cavanagh & Favreau, 1980) but the cyclopean MAE should not. However, the Patterson framework would predict no interaction between stimulus type and test pattern type: when going from standard-image test pattern to mirror-image test pattern, both cyclopean and luminance MAEs should decline similarly.

CHAPTER TWO

METHODS

Observers

Ten participants, ages 18 or older, served as observers in this study. All observers had normal or corrected-to-normal visual acuity, normal binocular vision and normal phoria (as determined by testing using a Bausch and Lomb Orthorater). All observers gave documented informed consent prior to participation.

Stimuli and Apparatus

The adapting stimulus was a cyclopean or luminance spiral pattern which was rotated expansively at a rate of 20 rpm (a preliminary experiment showed that this rate of spiral motion induces robust cyclopean and luminance MAEs, and it is similar to the rotational rate used by Cavanagh and Favreau), displayed on a Sharp monitor. The spiral pattern was created with the expression $r = e^\theta$, where r is the radius of the pattern and e^θ is an exponential function of θ to base e (Cavanagh & Favreau, 1980)². At the beginning of adaptation on each trial, the starting phase of the spiral was random. The test stimulus was a stationary spiral pattern which was either a non-mirror image (standard) or a mirror-image of the adapting pattern. Figure 1 provides examples of the spirals used for stimuli as adapt and test patterns.

² The author would like to thank Jim Gaska for assisting in the creation of the spiral images using MatLab software (The MathWorks, Inc).



Figure 1. Diagram of the spiral stimulus patterns. Figure 1a depicts the adapting pattern and the standard-image test pattern. Figure 1b depicts the mirror-image test pattern. Figure 1c depicts the mirror-image test pattern superimposed on the standard-image test pattern, demonstrating the existence of 90-degree angles at each of the intersections.

The cyclopean spiral patterns were composed of random dot textured areas that appeared to protrude in depth with a disparity of 11.4', crossed from the display screen, which alternated with areas appearing in the plane of the display screen with zero disparity (average disparity of the spiral were 5.7'). The luminance spiral patterns were composed of solid black areas which alternated with areas whose regions were filled with red-pixel noise, thus the luminance spiral was defined by differences in luminance, texture, and hue, all of which were presented with zero disparity.

The cyclopean stimuli were created with a dynamic random-dot stereogram generation system (Shetty, Broderson & Fox, 1979). The display device was a 19-inch Sharp color monitor with a refresh rate of 60 Hz, an overall display luminance of 25.2 cd/m², and a dot density of 50%. At a viewing distance of 160 cm, the angular size of the display subtended 14.25 x 10.71 deg. On this monitor, matrices of red and green random dots were displayed (approx. 5000 dots per matrix). Observers wore glasses containing red and green chromatic filters so that each eye views only one matrix of dots. The mean luminance of the red and green half-images through the filters was 3-4 cd/m².

A stereogram generator (analog computer) controlled the red and green guns of the Sharp monitor in order to display the red and green dot matrices. To create disparity, the stereogram generator laterally shifted a subset of dots in one eye's view, red or green, and left unshifted corresponding dots in the other eye's view. The gap created by the shift was filled with randomly positioned dots of the same density and brightness so that no monocular cues were visible. All dots in both matrices were replaced dynamically at 60 Hz, so that the cyclopean spiral patterns could be exposed and moved without monocular cues.

Signals from a black and white video camera, hidden from the observer's view, provided input to the stereogram generator, which determined where disparity was inserted into the stereogram. The camera scanned images of spiral patterns displayed on a ViewSonic VX724 LCD monitor, which were converted into cyclopean spiral patterns on the Sharp monitor.

The luminance stimuli were spiral patterns, which were composed of black areas that alternated with areas of red-pixel noise, and were created with the stereogram generation system and were also displayed on the Sharp monitor. The luminance of the red areas was 6.5 cd/m^2 , and the luminance of the black areas was 0.04 cd/m^2 .

The angular size of the spiral patterns across all conditions was 7.15 degrees.

Procedure

This study involved a 2 (stimulus type, cyclopean vs. luminance) x 2 (type of test pattern, standard-image vs. mirror-image) factorial design, which created four experimental conditions. On each trial, the observer adapted to the expansive motion of a

rotating spiral, cyclopean or luminance, for a duration of one minute. Following adaptation, the observer viewed a stationary test pattern (spiral) whose presentation was signaled by a sound from a computer. The observer was then asked to indicate the duration of the MAE by pressing a button on a computer keyboard when the illusory movement had appeared to cease. The observer was then given a one minute rest before the beginning of the next trial to minimize the threat of any lingering adaptation effects from the previous trial. Each observer participated in a single one-hour session of 16 trials, with four trials being collected under each of the four conditions. The order of the trials were randomly determined for each observer.

CHAPTER THREE

RESULTS

The four individual MAE durations collected under each condition for each observer were averaged together to provide an estimate of MAE duration for each condition. The results are shown in Figure 2, which depicts MAE duration (seconds) on the ordinate and type of test pattern on the abscissa, for both cyclopean and luminance domains. The figure shows that the aftereffect duration for the mirror-image test pattern declined by 20% relative to the standard-image test pattern. This decline occurred equally for both the cyclopean and luminance domains.

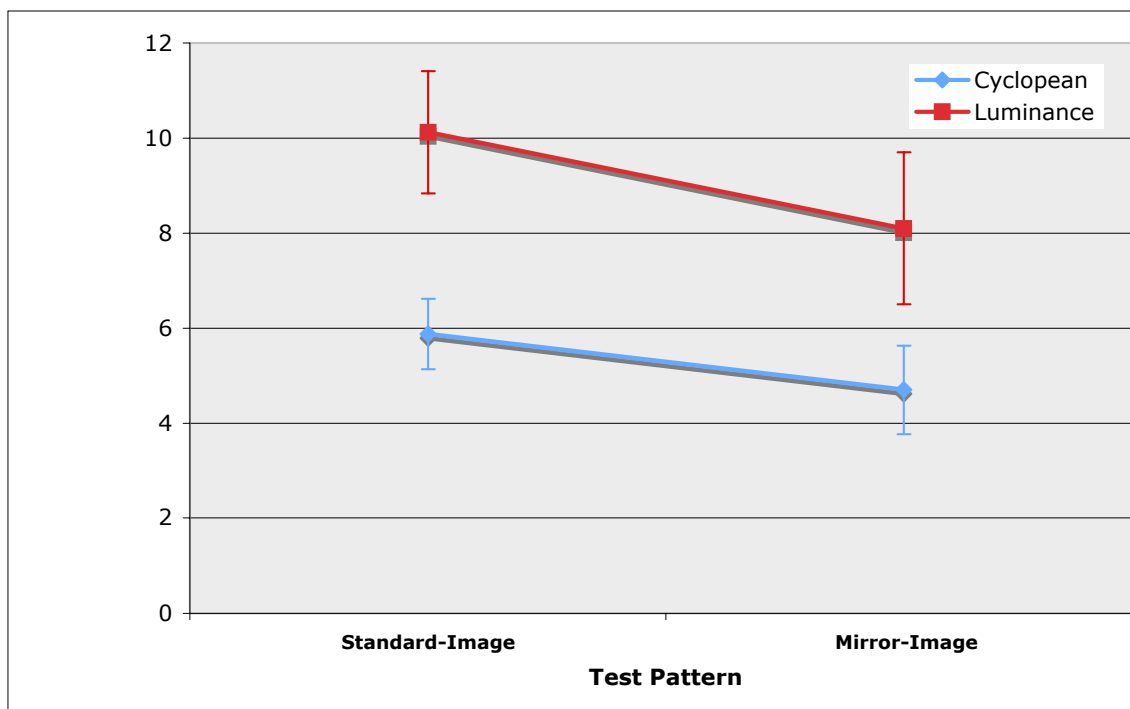


Figure 2. Mean MAE duration for the standard-image and mirror-image test patterns, for cyclopean and luminance stimuli. Each data point is the mean of 10 observers. Each error bar represents \pm one standard error of the mean.

These data were analyzed by a 2x2 analysis of variance (ANOVA) for within-subjects designs. This analysis showed that the effect of test pattern (mirror-image vs. standard-image) was significant, $F(1,9) = 7.853$, $p = 0.021$, with mirror-image test patterns having shorter MAE durations than standard-image test patterns. Also, the effect of stimulus domain (cyclopean vs. luminance) was significant, $F(1, 9) = 15.57$, $p = 0.003$, resulting in overall shorter MAE durations with cyclopean domain stimuli.³ There was no significant interaction between stimulus domain and test pattern $F(1, 9) = 1.656$, $p = 0.23$.

³ To rule out a floor effect with the one minute duration cyclopean adapting-stimulus, we also ran trials with a three minute duration cyclopean adapting stimulus, with all 10 subjects; according to Bowd et al (1996), a three minute adapting duration with cyclopean stimuli should make the MAE duration similar to the MAE duration induced with a one minute adapting duration with luminance stimuli. Then we combined these cyclopean trials with the luminance trials that are shown in Figure 2, and computed a 2x2 ANOVA for within-subjects designs. These analyses showed that the effect of test pattern (mirror-image vs. standard) was again significant ($F[1,9] = 21.494$, $p = 0.001$), with the mirror-image test pattern eliciting a shorter MAE duration (mean duration with the cyclopean mirror-image test pattern was 12.625 seconds; mean duration with the cyclopean standard-image test pattern was 14.525). There was no effect of domain ($F[1,9] = 2.78$, $p = 0.129$), as predicted. Additionally, there was no interaction of stimulus pattern and domain ($F[1,9] = 0.008$, $p = 0.930$). This shows that the trend shown in Figure 2 involving the cyclopean stimuli is not particular to a one minute adapting duration.

CHAPTER FOUR

DISCUSSION

This study employed a spiral motion aftereffect (MAE) paradigm, developed by Cavanagh and Favreau (1980), which involved the use of a mirror-image (reflected) test pattern during the test phase of an MAE. When the mirror-image test pattern was used, the duration of the cyclopean MAE declined, as did the duration of the luminance MAE, relative to when the standard (non-mirror-image) test pattern was used. These results are taken as evidence for multiple stages of motion processing for both luminance and cyclopean stimuli.

Recall from the introduction that Cavanagh and Favreau (1980) dissociated local, lower-level MAEs from global, higher-level MAEs through the use of a mirror-image test pattern, which contained 90-degree angles at every intersection when superimposed on the standard test pattern. Cavanagh and Favreau's logic was that if MAEs are produced by multiple stages of processing, then the use of a mirror-image test pattern should cancel the contribution of local motion mechanisms, leaving only the activity of global motion mechanisms. Thus, local is defined as orientation-selective and global is defined as orientation non-selective (Cavanagh and Favreau, 1980).

These authors found that the MAE duration was less with the mirror-image test pattern than with the standard-image test pattern, implying that the local mechanisms, which were cancelled with the mirror-image test pattern, typically yield longer aftereffects relative to the global aftereffects. Thus, when the local mechanisms were cancelled with the mirror-image test pattern, a shorter aftereffect occurred, which was assumed to be mediated by global mechanisms.

In the present case, our results show that the same logic can apply to cyclopean motion processing. When a cyclopean mirror-image test pattern is used, the contribution of local cyclopean motion mechanisms (which yield longer MAEs) would be cancelled, leaving only the activity of cyclopean global mechanisms (which would yield shorter MAEs). Indeed, it is known that local motion-sensing mechanisms are orientationally tuned in the cyclopean domain (Shorter, Bowd, Donnelly & Patterson, 1999). At the global level, presumably cyclopean motion-processing mechanisms would lose their orientation tuning, via spatial pooling, which could be considered a type of form-cue invariance (Albright, 1992). We therefore suggest that there are multiple stages of cyclopean motion processing.

Our results can be interpreted within a contemporary framework of the motion aftereffect (van de Grind, Lankheet & Tao, 2003; van de Grind et al., 2004). In this framework, the MAE is thought to arise from the disruption of the equilibrium of neural-network activity that signals different directions of motion. During the viewing of a moving adapting pattern, the network is shifted away from equilibrium, or set-point, due to a selective change in the gain of a subset of directionally-tuned cells. Next, when viewing a stationary test pattern, the disequilibrium provoked by adaptation will be reflected in the pooled output of motion-sensing cells, which causes an illusory perception of the test pattern moving in the opposite direction of the adapting pattern (i.e. MAE) (van de Grind et al., 2004). The duration of the MAE is thought to reflect the time taken for the gain of the adapted motion-sensing cells to recover back to their set-point level, and for the neural network to re-establish equilibrium.

This hypothetical sequence of events likely occurs at each of multiple levels of motion processing, such as local and global levels. However, in doing so, note that there is evidence that the time course of recovery from adaptation can be different at different levels of the motion stream. At lower levels of processing, the time course of recovery is more prolonged, leading to longer MAEs such as those that occur from viewing static test patterns (called sMAE). At higher levels of processing, the time course of recovery is relatively short, which yields brief MAEs (called dMAE), such as those that occur from viewing dynamic test patterns (Nishida & Sato, 1995). This implies that the time constants of exponential decay are longer at lower levels and shorter at higher levels (van de Grind et al., 2003; van de Grind et al., 2004).

Thus, at lower levels of motion processing, the recovery from adaptation can be summarized as following an exponential function, $\delta = e^{-t/a}$, where δ represents the MAE duration, and a represents the time constant for the decay rate which would be relatively long (e.g. 20 seconds), and t represents time since the end of adapting motion (van de Grind et al., 2003; van de Grind et al., 2004). Similarly, for higher levels of motion processing, the recovery from adaptation can be summarized with an analogous function, $\delta = e^{-t/b}$, where δ represents the MAE duration, b represents the time constant for the decay rate which would be relatively short (e.g. 12 seconds), and t again represents time since the end of adapting motion (van de Grind et al., 2003; van de Grind et al., 2004). Thus, our present results, and the results of Cavanagh and Favreau (1980), show that an analogous scheme would apply equally well to the distinction between local and global levels of processing, namely a longer time constant for local and a shorter time constant for global. Moreover, our results suggest that this scheme applies equally well to the

cyclopean and luminance domains, such that $a > b$, and $a/b = k$, where k is the same value for the luminance and cyclopean domains.

Turning now to the debate in the motion literature regarding stages of processing, recall that there are two competing theoretical frameworks, as discussed in the Introduction. These frameworks argue over the existence of a third-order motion mechanism. According to one framework by Lu and Sperling (1995, 2001), third-order motion detects objects as figure against ground, with cyclopean motion processing being solely a third-order process. This proposed system invokes the notion of a “saliency map” as an input to a system that employs an attentionally-gated high-level motion-energy computation. Furthermore, Lu and Sperling argue that third-order motion processing involves a process whereby, and importantly, motion information is globally pooled from lower-level (local) motion detectors, which is then passed onto higher-levels of the motion stream. However, according to the other framework by Patterson (1999, 2002), cyclopean motion is processed by a second-order system, rather than a third-order system, via front-end disparity detection followed by a motion-energy computation applied to the disparity domain. This processing is accomplished through the operation of relatively lower-level mechanisms that do not rely on pooling, visual attention nor feature tracking (Patterson et al., 2005)

The use of a mirror-image test pattern allows for testing of one property of the Lu and Sperling third-order motion system, namely the pooling of local signals onto global mechanisms. Since they claim that third-order motion mechanisms are global in nature, and that cyclopean motion processing is achieved solely via a third-order motion mechanism, then a mirror-image test pattern should produce a cyclopean MAE duration

equivalent to a standard test pattern. However, it does not. Instead, we find that using a mirror-image test pattern produces a shorter cyclopean MAE duration. This implies the existence of a local level and a global level of cyclopean motion processing, with the local level consistent within the Patterson framework and the global level consistent within the Lu and Sperling framework.

In summary, properties of gain control mechanisms at binocular levels of vision appear to be analogous to those at lower visual system levels, thus reinforcing the idea of conservation of computation.

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