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STATIC AND DYNAMIC MOTION AFTEREFFECTS OF FIRST- AND SECOND-ORDER MOTION IN CENTRAL AND PERIPHERAL FIELDS OF VISION

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ABSTRACT

Static and Dynamic Motion Aftereffects of First-and Second-Order

Motion in Central and Peripheral Fields of Vision

Armando Bertone

After prolonged adaptation to a moving pattern, a subsequently presented static or dynamic test pattern will appear to drift in the opposite direction. This illusory drift is referred to as the motion aftereffect (MAE). It is well accepted that a MAE is not elicited after adaptation to second-order motion if tested with a static test (sMAE), although a clear MAE is perceived if tested with a dynamic pattern (dMAE), which is believed to access higher levels of motion processing. These second-order MAE properties, in part, have led to motion-detection models postulating that first- and second-order motion are processed, at least initially, by separate mechanisms. The purpose of the present study was to define the MAE properties of second-order motion in the periphery in order to evaluate the exclusiveness of the second-order MAE properties to central vision. Observers were adapted to non-scaled second-order patterns at fixation and in the periphery (up to 12°) and tested with both static and dynamic test patterns. Results showed that for all observers, a same was perceived after second-order adaptation in the periphery, although none was elicited after central adaptation. This suggests the existence of different motion mechanisms operating in central and peripheral visual fields; separate mechanisms sensitive to each motion type in the central visual field and a common, low-level mechanism mediating both first- and second-order processing in the periphery. Additional results obtained from preliminary studies comparing first- and second-order motion sensitivity across eccentricity also provide evidence that first- and second-order motion processing may be mediated by a different mechanism in the periphery than at fixation. The possible effects of spatially scaling the patterns as well as more direct methods to address the underlying peripheral mechanisms are discussed.

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Visual Motion Perception

More often than not, objects of importance in our environment are in motion. We perceive these moving objects unconsciously, able to immediately determine their direction and speed with great precision. The ease with which we are able to perceive moving objects reflects the adaptive importance of motion perception, the underlying mechanisms of which have evolved into an incredibly efficient system. Basically, we must be able to recognize the objects in our environment and where they are located in order respond adaptively with respect to them. Usually, however, it is more important to know where an object is going or coming from than to just know its location. For example, it is more informative for an animal to perceive a predator moving towards it than to simply perceive it at rest. Similarly, when deciding to cross a busy street, a pedestrian's decision is based more on moving cars compared to cars parked on the curb. The ability to detect motion information is integral for the survival of any sighted animal, including ourselves.

As stated by Marr (1982), 'Visual motion is just one piece in the puzzle of the reconstruction of the external world'. Compared to other visual functions, research within the area of motion processing has developed particularly rapidly (Smith, 1994). The interest in motion perception research can be attributed to its involvement in many perceptual functions (see Nakayama, 1985 for review). The importance of motion perception is also evidenced by the existence of distinct neurons found in cortical areas of the primate devoted to the processing of motion information (e.g., Zeki, 1974; 1978). This degree of specialization is also suggested by clinical studies where damage to motion detecting cortical areas (e.g., medial temporal (MT) area) results in the inability to process

motion information. Patients with these selective lesions are literally 'motion-blind' since they are not able to perceive moving objects while other visual functions are relatively unaffected (Zihl et al., 1983).

Although these electrophysiological and clinical studies provide convincing evidence of a specialized motion processing system, probably the oldest demonstration of such a system is phenomenological in nature and is referred to as the Waterfall Illusion. Since its discovery, the Waterfall Illusion has been used by psychophysicists as an investigative tool, a means of measuring motion processes at different sites along the visual motion pathway. The present study, like many others before it, will use this to investigate the characteristics of two motion types, first- and second-order motion, in both peripheral and central visual fields.

The Waterfall Illusion

'Visual illusions reveal visual truths' (Purkinje, 1825). Over 170 years after this statement was voiced, illusions are still being used as investigative tools in vision research. One visual illusion that has been used extensively in visual motion research has been the Waterfall Illusion. This motion illusion was initially reported by Addams (1834), who after looking at a waterfall for a prolonged period of time, perceived stationary objects, such as adjacent rocks, to move in the opposite, upward direction. This illusion has a long history, documented at least since the time of Aristotle (ca300BC) and others in the nineteenth century (e.g., Purkinje; 1825; see Wade, 1994). Today, it is referred to as the motion aftereffect (MAE), a more general term reflecting the general types of stimuli by which it can be elicited.

The Motion Aftereffect (MAE)

After prolonged adaptation to unidirectional motion, a subsequently presented stationary pattern will appear to drift in the opposite direction (Wohlgemuth, 1911). Similarly, the movement within a directionally-ambiguous test pattern (e.g., counterphasing grating) will also appear opposite to the adapting direction (e.g., Levinson & Sekuler, 1975; von Grünau, 1986; Bertone & von Grünau, 1997).

Modern day interpretations of the MAE started to emerge only after physiological studies revealed that an overwhelming number of cells in a variety of visual structures responded vigorously to moving patterns (Nakayama, 1985). Since its initial comprehensive examination by Wohlgemuth (1911), the MAE has been used to investigate the mechanisms of motion perception because it is generally assumed that a MAE is the result of adaptation of motion-selective structures in the visual system. Explanations of the neural mechanisms of the MAE have been based mainly on two models known as the Ratio-model and Distribution-Shift model.

Neural Mechanisms of Motion Aftereffect

The Ratio-models of Sutherland (1961) and Barlow and Hill (1963)

Arguably, the most important neurophysiological discoveries in vision research were made by Hubel & Wiesel (1959, 1962, 1965) who showed that most cells in the cat primary visual cortex were selective to the orientation of luminance-defined contours and to the direction of their movement. Based on these findings, Sutherland (1961) was the first to offer a neural explanation for the MAE, suggesting that neural fatigue, caused by the continuous adaptation of the direction selective neurons described by Hubel and Wiesel, may underlie the production of the MAE.

Sutherland proposed his Ratio-model for coding the direction of visual motion and the underlying physiological framework of the MAE. According to his model, the direction in which a stimulus is perceived to move depends upon the ratio of activity of directionally selective, motion-encoding neurons, or motion detectors (please see *Review of Computational Models of Motion Detection*) tuned to opposing directions. For example, for leftward motion to be perceived, the activity of neurons selective to leftward motion have to exceed the activity of rightward selective neurons by a minimum ratio. However, during prolonged adaptation to one motion direction, only the neurons selective to that motion are excited and consequently fatigued while others selective to the opposite, or 'null', direction are unaffected and fire only spontaneously. Upon cessation of adaptation, the excited neurons will fire at a reduced rate (below spontaneous activity), allowing the neurons tuned to the opposite direction to temporarily exceed the minimum ratio needed to perceive motion, even if the stimulus is stationary. According to the Ratio-model, this temporary imbalance in the activity between the oppositely tuned neurons is the neural basis of the MAE.

> *'... the direction in which something is seen to move might depend upon the ratios of firing in cells sensitive to movement in different directions, and after prolonged movement in one direction a stationary image would produce less firing in the cells which had just been stimulated than normally, hence apparent movement in the opposite direction would be seen to occur.' (Sutherland, 1961, p.227)*

Electrophysiological support for Sutherland's speculations was provided by Barlow and his colleagues (Barlow & Hill, 1963a; Barlow et al., 1964). Recording from motion selective ganglion cells in the rabbit retina, they found that after stimulating a neuron with movement in its 'preferred' direction, its discharge dropped below baseline activity upon cessation of movement. As a result, the spontaneous activity of the unstimulated neurons tuned for the opposite 'null' direction was relatively higher. The activities of the stimulated

(firing below baseline) and the non-stimulated (responding spontaneously) neurons became unbalanced, resulting temporarily in an illusory motion opposite the adapted direction; the MAE (see Figure 1).

Problems for the Ratio-models: Bivectorial and Transparent Motion

The Ratio-models of Sutherland (1961) and Barlow and Hill (1963a, b) provide a simple neural explanation for the coding of motion direction and MAE production. Basically, the MAE direction is always opposite the adapting direction, suggesting that only neurons tuned (or coupled) to opposite motion directions are involved in the production of a MAE.

The Ratio-models, however, are limited in that they do not predict the resultant MAE direction of bi-vectorial or transparent (Clarke, 1977) motion. These are situations where motion in two different directions are presented either successively, in alternation, or simultaneously at the same spatial location. If two distinct and separate motion directions are perceived during adaptation, the Ratio-models should predict two individual MAEs, one opposite to each of the perceived directions. This, however, is not what is perceived. Rather, after adaptation to either successively (Levinson & Sekuler, 1976; Riggs & Day, 1980; Wenderoth et al., 1988; Verstraten et al., 1994a, b) or simultaneously (Mather & Moulden, 1980; von Grünau & Dubé, 1992; Verstraten et al., 1994a; von Grünau et al., 1998) presented bi-vectorial motion, the resulting MAE is unitary and directed opposite the vector sum of the adaptation motions (see Figure 2a).

Mather's (1980) Distribution-Shift Model

In an attempt to explain the unified MAE, Mather (1980) introduced his Distribution-Shift model for the coding of visual motion. Like the Ratio-model, motion detection is only possible when activity of neurons selective to the direction of a presented stimulus (target signal) exceeds the spontaneous activity of the remainder of the neurons
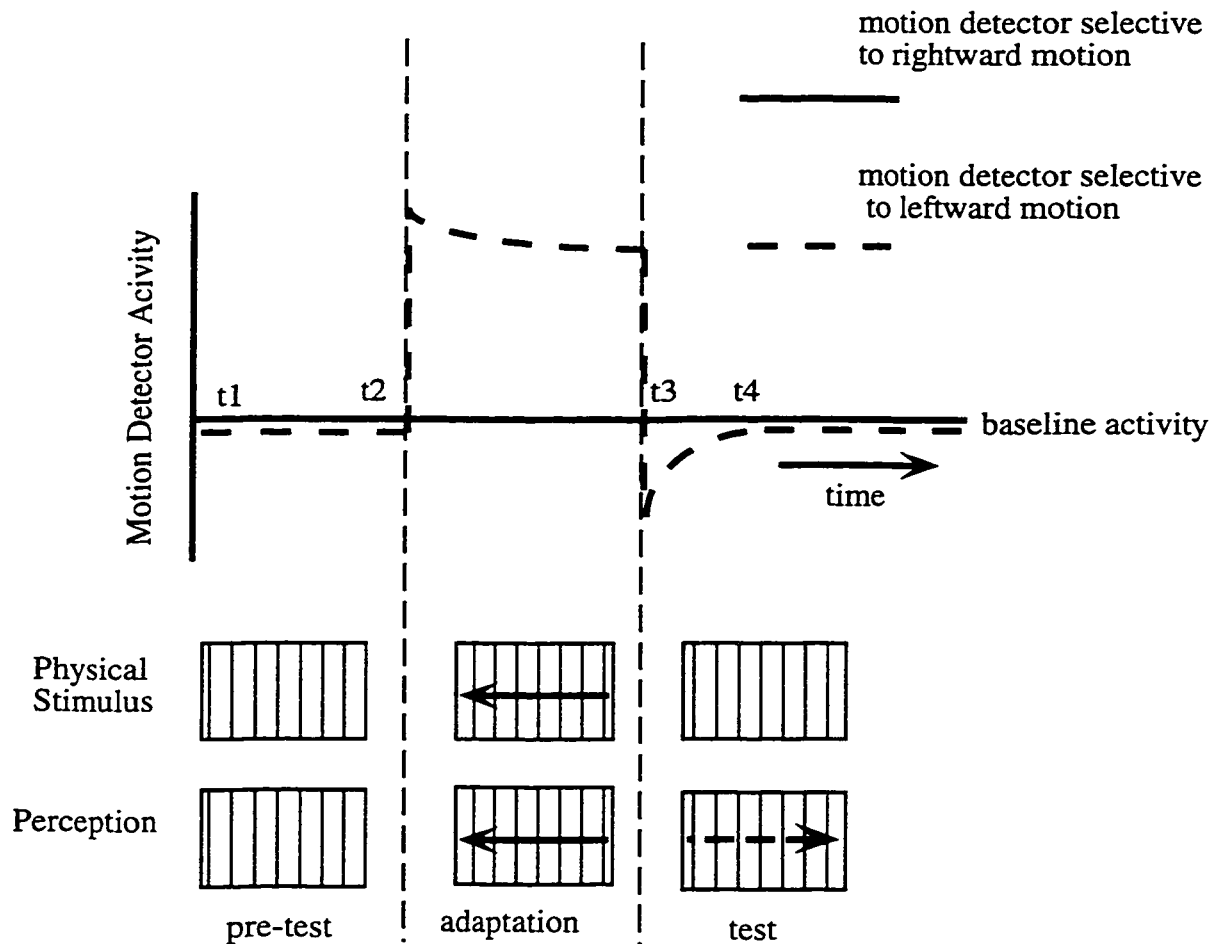
Figure 1. A schematic representation of the ratio-model. The dotted and solid lines represent the activity (firing rate) of directionally selective detectors. From time t1 to t2 no motion is perceived (motion detectors firing spontaneously during pretest). Adaptation to leftward motion from t2 to t3 results in an increase in firing of the selective motion detector. At time t3 adaptation is ceased, causing the firing rate of the 'fatigued' leftward selective detectors to be relatively below that of the rightward selective detectors, resulting in an MAE directed towards the right (test). Dissipation of MAE occurs from time t3 to t4.
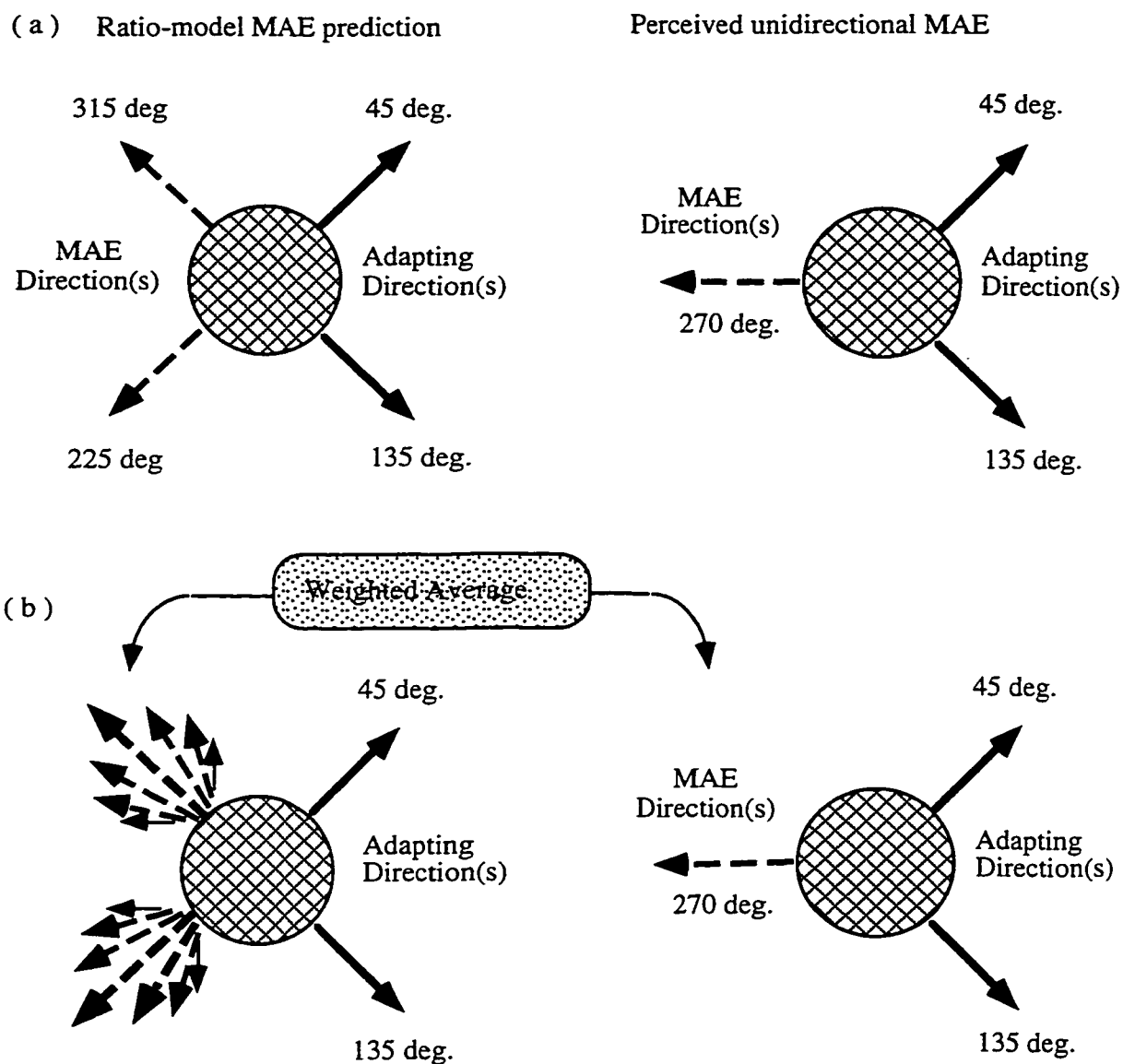
Figure 2. A schematic representation of the (a) Ratio model's MAE direction
prediction and actual MAE percieved direction after adaptation to bivectorial
motion and how (b) the Distribution-Shift model correctly predicts the direction
of the unidirectional MAE by weighing the responses of all neurons.

involved in the ratio comparison by a critical (signal-to-noise) ratio. The two models, however, differ with respect to the 'distribution' of activity assumed to be involved in the ratio comparison. Unlike the Ratio-model, the Distribution-Shift model proposes that integration of motion information takes place across all directions and not just across opponent pairs of neurons. For example, simultaneous adaptation to two orthogonally moving patterns (e.g., at 45 and 135 deg) will excite neurons selective for those two motion directions maximally as well as exciting those tuned to nearby directions to a decreasing extent the more their selective direction differs from the adapted directions (Blakemore & Tobin, 1972). The MAE direction is therefore opposite the weighted activity of all neurons, integrated across all orientations. When presented with a stationary test stimulus after adaptation to two transparently moving gratings at 45 and 135 deg, the Distribution-Shift model correctly predicts a unidirectional MAE, directed towards 270 deg (see Figure 2).

The Ratio and Distribution-Shift models offer simple explanations for the production of the MAE. Regardless of certain limitations, they are arguably still the best models currently available for explaining the compiled psychophysical MAE data, particularly for the bi-vectorial or transparent MAEs (Verstraten, 1994). At the least, they are the basis for more recent models attempting to explain the unitary nature of the MAE perceived after transparent motion adaptation (Grunewald & Lankheet, 1996).

Theoretical implications based on MAE studies are of great importance to the visual motion literature since it has been suggested that this motion illusion reflects the existence of directionally selective neurons in the visual system (Nakayama, 1985), the prolonged excitation of which result in a MAE. For this reason, hypotheses based on the Ratio and Distribution-Shift models (e.g., involvement of signal opponency in motion detection) have been incorporated in earlier, neurophysiological (Barlow & Levick, 1965) and contemporary, computational models of human motion perception (e.g., Adelson & Bergen, 1985; van Santen & Sperling, 1985).

It is unlikely, however, that individual directionally selective neurons are able to compute the direction of motion on their own (Grzywacz et al., 1994). This is reflected by the fact that motion detectability and direction predictability hypotheses of all current motion detection models are based on the combined outputs and comparison of these outputs of many (e.g., at least two) neurons. These theoretical motion-detecting units, referred to as motion detectors, are the basis of all motion detection models. The following section will introduce and review a few of the most pertinent computational models of early human motion perception currently available in the literature, the majority of which fall into Reichardt-Type or Motion-Energy classes.

Review of Computational Models of Motion Detection

The earliest algorithmic model (Marr, 1982) concerning motion detection was one proposed by Reichardt (1961), who initially introduced the concept of 'motion detector' as the basic motion-detecting unit to explain the optomotor behaviour of insects. This influential model, known as the Reichardt detector model, has been adopted as a working hypothesis for motion detection in the human visual system (Mather, 1990). In its simplest form, a Reichardt detector computes a direction-selective motion response by comparing temporally offset neural signals from two adjacent receptive field (RF) locations on the retina. Inputs from the two RFs converge at an interaction site, where the signals are multiplied and integrated. Directional selectivity is possible because of a spatial asymmetry, attributing different temporal characteristics to each input, introduced by delaying one of the signals before comparing them at the site of multiplication. As seen in Figure 3a, the signal coming from the left is delayed (Δt) relative to that coming from the center. Therefore, for rightward motion, the two signals will arrive at the site of multiplication at the same time (the earlier signal from the left is compensated with the delay) which results in a positive multiplication which in this case, signals rightward motion.
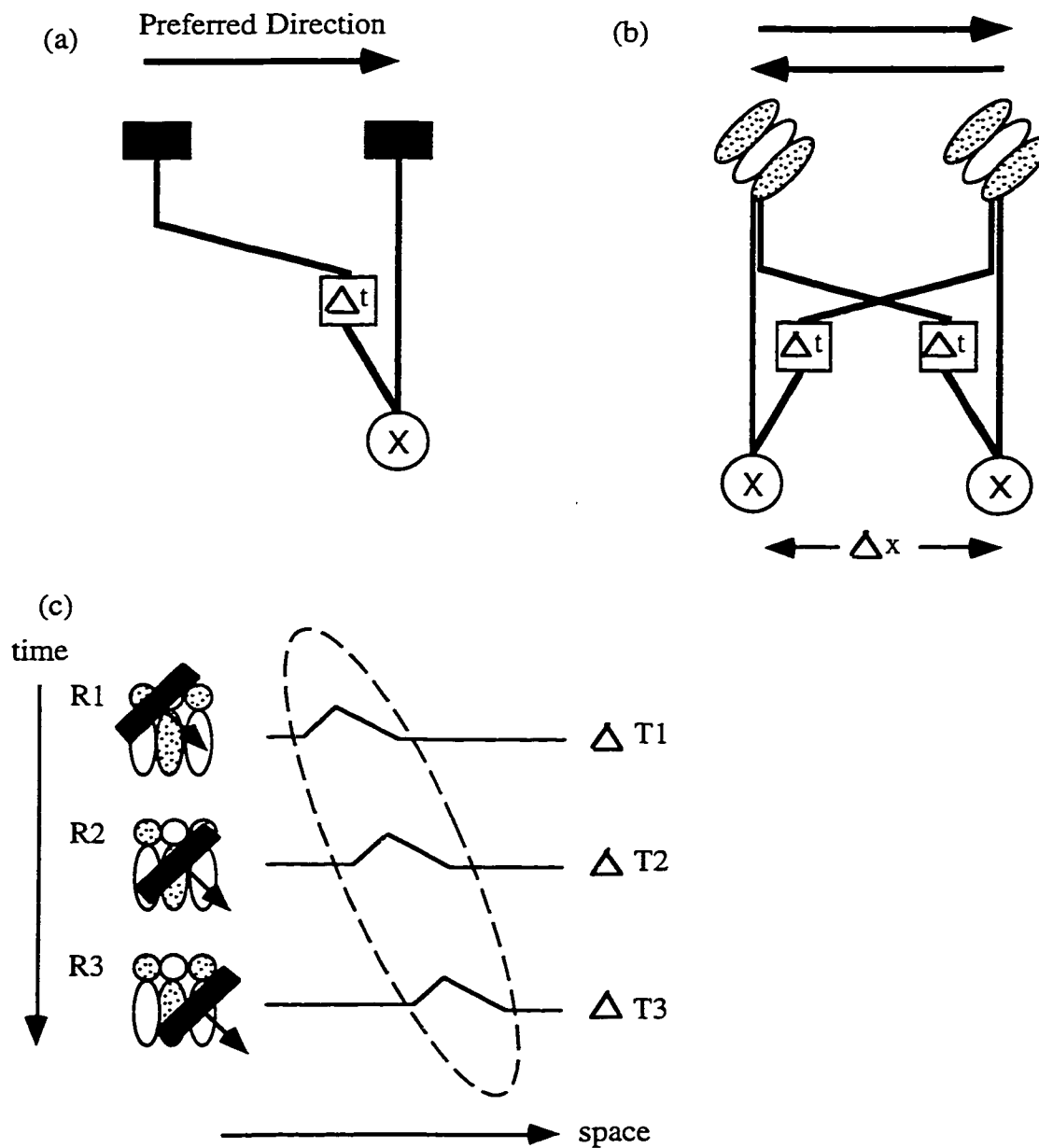
Figure 3. Schematic representations of (a) the basic Reichardt motion detector, (b) the Elaborated Reichardt motion detector (ERD) and (c) the directionally selective responses of the Motion-Energy model viewed in terms of a tilted receptive-field profile.

Based on Reichardt's motion detector, van Santen and Sperling (1985) proposed the Elaborated Reichardt Detector (ERD), which they argue is a more appropriate model for human vision, emphasizing the importance of both spatial and temporal filtering performed for each of the inputs, or receptors, before multiplication. The spatiotemporal filtering is important because it eliminates spatial aliasing which would otherwise result in incorrect direction prediction. These authors describe a drifting sinusoidal grating as being a temporal luminance pattern (e.g., sine wave) varying as a function of spatial location. Motion detection is carried out by comparing the delayed temporal luminance pattern of one output to that of the other non-delayed luminance pattern at the other spatial location. If the two signal outputs or intensities correlate well at the site of multiplication, the direction of the grating is detected. Essentially, the basic ERD model compares and integrates the responses of two spatial-frequency selective mechanisms displaced in time and space (see Figure 3b).

Motion-Energy models (Adelson & Bergen, 1985) are another important class of motion detection models. These models differ from the ERD model in that detection of motion direction is determined as orientation in space-time. The spatial asymmetry of motion-energy models is distributed across different locations in one receptive field instead of across two RFs. Consider, for example, a luminance defined contour moving across a receptive field of a motion-energy detector (see Figure 3c). If the contour is moving in the preferred direction, the region of the RF initially reached by the edge (R1) will respond first $(\Delta t1)$, followed by the response elicited by the next region (R2) (e.g., $\Delta t1 > \Delta t2 > \Delta t3$, etc.). Therefore, different spatial locations within the receptive field will elicit different time courses of responding. A space-time plot of the time course of responses of different positions of the RF reveals motion energy (the output of motion energy filters) at a certain spatiotemporal orientation which can be detected as motion by motion selective cortical cells.

The Elaborated Reichardt Detector and Motion-Energy models are just two of several computational models (e.g., Watson & Ahumuda, 1985) that provide systems theoretically capable of detecting motion directions. Most models share one important aspect; a low-level filtering stage where the analysis of Fourier or luminance-defined components of the motion signals, defined by local variations in retinal image intensity, occurs.

Measurement of the Motion Aftereffect

Static and Dynamic Tests

It has been suggested that the MAE ' is easy to record badly but hard to record well' (Anstis, 1986). Several methods have been adopted to measure the MAE, including several nulling (e.g., Wright & Johnson, 1985; von Grünau & Dubé, 1992; Ledgeway, 1994) and matching (e.g., Hiris & Blake, 1992) techniques. However, the index that has been used most often to measure the strength of a MAE has been its duration; the time the illusory drift takes to dissipate after cessation of adaptation (Wohlgemuth, 1911). In this case, a moving adaptation stimulus (e.g., a drifting sinewave grating) is replaced with the same pattern presented statically, referred to as the test (static sinewave grating) grating. The MAE strength is defined by the time the static test grating drifts in the direction opposite to that of adaptation. A MAE measured with a static test pattern is known as a 'classic' or static MAE (sMAE).

A MAE can also be observed when a directionally ambiguous moving pattern is used as a test stimulus (Levinson & Sekuler, 1975). The motion within the test stimulus will be perceived to move coherently in the direction opposite to adaptation until dissipation of the MAE, reflected in the return of ambiguity of motion perceived within the test stimulus. Examples of dynamic test stimuli are counterphasing luminance gratings (e.g.,

von Grünau, 1986; Nishida et al., 1994; von Grünau et al., 1998), randomly moving dots (e.g., Blake & Hiris, 1993), patternless sinusoidal flicker (Green et al., 1983) and dynamic random-pixel arrays (RPAs) (e.g., Verstraten et al., 1996). A MAE measured with a dynamic test is referred to as a flicker or dynamic MAE (dMAE).

Perceptually, obvious differences exist between static and dynamic MAEs. Firstly, the illusory motion of a sMAE is different from that of the real, adapting motion. For example, after adapting to a translating grating, the subsequent static test pattern appears to drift in the opposite direction. The real and subsequent illusory movements are easily distinguishable, creating a paradox of sorts; the observer knows the test pattern is stationary but still must make a judgment on when the illusory movement ceases. On the other hand, the biased movement perceived within a dynamic test (e.g., counterphasing grating) is perceptually comparable to the preceding real motion (Levinson & Sekuler, 1975; Hiris & Blake, 1992). Another difference is perceived during the time course of the illusion. A very strong (high velocity) sMAE is initially perceived opposite the adapting direction and dissipates gradually with time until the illusory motion is no longer seen. The strength of a dMAE, however, seems to be more constant throughout its time course. For example, if testing with a counterphasing grating, the end of the dMAE is perceived immediately, defined by the return of ambiguity of motion within the test stimulus. During the dMAE, the motion within the stimulus is either biased or not biased; no varying degree of biased is perceived. Therefore, although relatively shorter lasting (Green et al., 1983; Verstraten, 1994), the MAE induced using dynamic test stimuli appears more salient.

Recently, differences in the two MAE have taken on more theoretical significance. Although both MAE types are believed to be the result of the adaptation of directionally selective visual mechanisms, many studies using luminance-defined motion stimuli (e.g., sinewave gratings or RPAs) have demonstrated qualitative differences between MAEs measured using static tests and those measured using dynamic tests. These differences are of interest because it is generally thought that the type of test pattern used might reveal

different sites of adaptation along the path of visual motion processing (Hiris & Blake, 1992; Nishida & Sato, 1995).

The following section will summarize some selected stimulus properties that influence the strength of both static and dynamic MAEs as well as some qualitative differences between MAEs measured after adaptation to luminance-defined (or Fourier) stimuli.

Qualitative MAE Differences Using Static and Dynamic Tests

Many studies have shown that the strength of static and dynamic MAEs differ quantitatively when parameters of either the adaptation or test stimuli are systematically varied. It has been shown, for example, that luminance contrast of either the adaptation or test stimulus influences the duration of both static and dynamic MAEs in a similar way. Specifically, the MAE strength, measured by duration, increases with increasing adaptation contrast or decreasing test contrast (Keck et al., 1976; Nishida et al., 1997a). Spatial and temporal stimulus properties also influence MAE strength of both types. Static MAE seems to be spatial-frequency selective because it has been shown that the adaptation strength is strongest when the spatial frequency of adaptation and test stimuli is matched (Over et al., 1973; Cameron et al., 1992). Dynamic MAEs, however, appear to be mediated to a greater extent by the adapting velocity of the adaptation stimulus (Ashida & Osaka, 1995), regardless of its spatial characteristics (Ashida & Osaka, 1994).

Recent interocular transfer (IOT), spatial specificity (retinotopic) and attention-based motion studies have provided robust, qualitative distinctions between static and dynamic MAE characteristics after luminance-defined adaptation.

A static MAE is usually only measurable when the adapting and test patterns are presented at the same retinal location since both patterns are stimulating the same neurons (Anstis & Gregory, 1965). Using a dynamic test, von Grünau and Dubé (1992) were able to measure a remote aftereffect; a dMAE in a spatial location which was not stimulated

during adaptation. These authors have suggested that the remote MAE arises in extrastriate areas (MT or MST) where RF sizes are much larger than those found in V1. Furthermore, they suggested that testing with dynamic stimuli may simply be a more sensitive technique for measuring weaker effects given that a dynamic test has components drifting in the MAE direction.

Psychophysical techniques can be used to make inferences concerning the level at which adaptation occurs within the visual system. One technique used to investigate the level of motion processing involves measuring the interocular transfer (IOT) of an aftereffect, the extent to which adaptation in one eye produces an aftereffect in the other eye. For example, complete IOT suggests adaptation is taking place at a higher level, where binocular signals are predominant (e.g., MT). Most IOT studies have shown that the transfer of sMAE after adaptation to luminance-defined motion is partial (e.g., Mouldon, 1980; Blake et al., 1981). Nishida et al. (1994) reexamined the IOT using both static and dynamic test patterns after adaptation to square-wave luminance gratings. They found that, as expected, the sMAE transferred only partially. Testing with a dynamic counterphasing pattern, however, a 'nearly perfect' transfer of the MAE was found. Based on their findings, they suggested that the differences in the magnitude of transfer between the sMAE and dMAE might reflect different levels of motion processing along the visual pathway; the sMAE reflects the adaptation at a lower-level of processing whereas the dMAE reflects a higher-level of motion processing.

Traditionally, the MAE has been thought to be a 'pre-attentive' phenomenon, unaffected by the attentional state of the observer (Wohlgemuth, 1911). However, several studies have reported modulation of the duration and direction of MAEs after allocation of attention to different areas (Chaudhuri, 1990; Takeuchi & Kita, 1991) or different components (Lankheet & Verstraten, 1995; von Grünau et al., 1998) of the adapting stimulus. A study by Culham and Cavanagh (1994) investigated the effect of attentive tracking of a counterphasing radial grating on subsequent static and dynamic MAEs using a

nulling technique. Results showed that attentive tracking of one of the components elicited a dMAE opposite the attended direction but no sMAE. The lack of a sMAE after attentive tracking suggested that the properties of the two MAE types may differ with regard to their ability to measure or access the consequence of adaptation to motion thought to be processed at higher levels.

Do Different Test Types Access Different Levels of Processing ?

Basically, static and dynamic tests appear to differ qualitatively in their ability to access higher-level motion processing mechanisms, such as those involving attention or binocular processing. The quantitative and qualitative differences in strength and origin between the two MAE types after adaptation to luminance-defined motion mentioned in the preceding section make it difficult to argue against the existence of separate mechanisms mediating the two MAE types. Based on the growing evidence showing their different characteristics, the notion that dMAE is simply the result of a more sensitive testing technique (Cavanagh & Mather, 1989; von Grünau & Dubé, 1992) has been rejected and replaced with the hypothesis that the two types of MAE reveal different levels of motion processing (e.g., Nishida & Sato, 1995). The most recent and probably the most theoretically important evidence supporting this hypothesis has come from studies investigating the differential adaptation to first- and second-order motion (Cavanagh & Mather, 1989).

What are first- and second-order motion?

Long- and Short-Range Motion

Braddick (1974) was the first to suggest that human motion perception might involve two distinct motion detecting systems. By varying spatial and temporal properties

of dot displacements within random dot kinematogram (RDK) displays, Braddick defined spatial displacement limits, defined as *d max*, above which the perception of apparent motion (Exner, 1888; Wertheimer, 1912) ceased. Based on his experimental findings, two types of motion processes where introduced, defined by their spatio-temporal characteristics; a 'short-range' process which operates over short spatial displacements and brief inter-stimulus intervals (ISI) and a 'long-range' process which operates over longer displacements and ISIs.

Of more theoretical importance, the two motion processes were believed to be mediated by qualitatively different motion extraction mechanisms (Braddick, 1980; Anstis, 1980) with short-range motion processing being carried out at a low level of motion processing (e.g., by Elaborated Reichardt Detectors) and long-range motion processing taking place at a higher level, perhaps mediated by cognitive processes beyond the responses of conventional motion detecting systems (Braddick, 1980; Anstis, 1980; Cavanagh, 1992). Empirical evidence has been put forth to distinguish properties of the 'long' versus 'short' range mechanisms (see Cavanagh & Mather, 1989).

Reviewing evidence of their own, Cavanagh and Mather (1989) challenged the dichotomy put forth by Anstis (1980) and Braddick (1980), arguing that the original distinctions based on the spatiotemporal properties were more attributable to the discrepancy between the stimuli used in short- and long-range experimentation rather than the type of mechanism used to process the information. Furthermore, they cited studies which failed to support the original criteria for distinguishing between the two motion processes. One such defining criterion was the inability of 'long' range motion to produce a MAE (Anstis, 1980), interpreted as evidence against 'long' range motion being mediated by low-level mechanisms. von Grünau (1986), however, showed that a 'long' range MAE exists if tested with a directionally-ambiguous, dynamic test pattern instead of the more conventional stationary test.

Based on their accumulated evidence against a 'long' versus 'short' range dichotomy, Cavanagh & Mather (1989) proposed a new distinction of motion processing which emphasized motion stimulus attributes; one of first-order versus second-order.

First- and Second-Order Motion

Usually, the contour of the object is defined by a difference in luminance with respect to its background (e.g., luminance step). When the object moves, so does its contour, which is cast across the retina of the observer. According the Cavanagh and Mather (1989), this is an example of a first-order motion defined by the coherent spatiotemporal displacements of the luminance on the retinal image. Second-order motion, however, is defined by displacements of stimulus characteristics other than luminance. For example, if an object and its background have the same mean luminance but differ in the distribution of luminance over their area, movement of the stimulus will not result in a coherent displacement of luminance over time. Chubb and Sperling (1988) defined the motion of such stimuli as 'drift-balanced' because the motion energy of second-order stimuli is equal in opposite directions. They also refer to this class of stimuli as 'non-Fourier' because the Fourier components of 'drift-balanced' stimuli cannot be used to predict the perceived direction of motion using low-level, energy-based motion detectors.

The study of second-order motion processing is of theoretical importance because energy-based motion-detection models, such as the ERD or Motion-energy models, are based on detection mechanisms which respond to net directional motion energy. Theoretically, these detectors are not able to extract the directional information of 'drift-balanced' stimuli. Regardless, second-order motion is readily perceived.

The following sections will review psychophysical studies examining MAE after adaptation to second-order motion. Results from these and other studies have been used as evidence as to whether or not first- and second-order stimuli are processed by a common or separate mechanisms.

Selective Adaptation Studies to Second-Order Stimuli

Since being defined (Cavanagh & Mather, 1989), several studies have examined MAEs following adaptation to different types of second-order stimuli, including frequency-modulated (e.g., Turano & Pantle, 1989) and contrast-modulated noise (e.g., Ledgeway, 1994). These studies have shown that after adaptation to second-order motion, testing with a static pattern results either in a relatively weak MAE or no MAE at all (e.g., Anstis, 1980; Anstis & Mather, 1985; Derrington & Badcock, 1985; Mather, 1991; Nishida & Sato, 1992; Ledgeway, 1994), depending on the type of second-order adaptation stimulus being used. The literature abounds with such evidence and it is now well accepted that second-order motion does not produce a convincing sMAE.

Adaptation Studies Using Static and Dynamic Tests

Is the lack of a sMAE following second-order adaptation a consequence of the adapting pattern characteristics or does the type of test stimuli used to measure the adaptation influence its production? This question was examined by McCarthy (1993) who found that after adaptation to the motion of a contrast-modulated sinusoid, a MAE was elicited only when tested with a dynamic stimulus. Converging evidence was found by Ledgeway and Smith (1994). After adapting observers to second-order motion (contrast-modulated noise), the duration of the subsequent MAE was measured using directionally-ambiguous first- or second-order motion patterns. Their results confirmed those of McCarthy (1993), showing that adaptation to second-order motion results in a clear MAE only if a dynamic test pattern is used.

In a similar study, Ledgeway (1994) found that as with first-order adaptation, the magnitude of the second-order MAEs was dependent on the relative contrasts (modulation depths) of adaptation and test stimuli (Keck et al., 1976). For example, if the depth of contrast modulation of the second-order adaptation pattern was lower compared to its test,

the adaptation elicited a weaker MAE than if both adaptation and test stimuli had the same contrasts. In addition, when equated for visibility, cross adaptation between first- and second-order motion stimuli (e. g., first-order adaptation with second-order test) produced MAEs of similar magnitude compared to same-adaptation (e.g., first-order adaptation with first-order test) conditions when measured using either a nulling technique (Ledgeway, 1994) or by MAE durations (Ledgeway & Smith, 1994b).

Selective adaptation studies using the 'threshold-elevation' technique as a measure of adaptation have also shown cross-adaptation effects between first- and second-order motion. Turano (1991) found that after prolonged adaptation to a drifting first-order grating, the threshold contrast needed for motion detection in the same direction increased not only for a subsequently presented first-order test, but also for a second-order test. Therefore, the results indicated that adaptation to first-order motion affects second-order motion detection, and vice versa. These results were interpreted by Turano as evidence for a common mechanism mediating both first- and second-order motion detection.

Although the cross-adaptation effects found by Turano (1991), Ledgeway (1994) and Ledgeway and Smith (1994) appear to suggest a common motion detecting mechanism for both motion types, most of the recent psychophysical evidence (e.g., Harris & Smith, 1992; Mather & West, 1993; Ledgeway & Smith, 1994a; Nishida et al., 1994; Nishida & Sato, 1995; Verstraten et al., 1996) suggests that at least initially, first-and second-order motion are processed by separate mechanisms (e.g., Chubb & Sperling, 1988; Wilson et al., 1992; Nishida & Sato, 1995; Nishida et al., 1997b). Furthermore, it can be argued that the aforementioned cross-adaptation effects could be the result of the high-level integration of signals originating from separate low-level mechanisms, and not the result of a common processing mechanism (Smith, 1994).

Models of Second-Order Motion Processing

As mentioned earlier, most current models of motion detection include a low-level spatiotemporal filtering stage where the analysis of Fourier or luminance components of the motion signal takes place. These models, however, are theoretically incapable of processing second-order motion because stimuli defining second-order motion do not contain net directional motion energy, e.g., 'non-Fourier motion' (Chubb & Sperling, 1988). This is evidenced psychophysically in that a MAE is not elicited after adaptation to second-order motion when tested with a static pattern, a test considered to reflect the adaptation of low-level motion mechanisms. Where and how then, is second-order motion detected?

As outlined by Smith (1994), the two possible strategies our visual mechanisms might adopt to detect second-order motion are defined by correspondence- and energy-based models. Correspondence-based models are based on the matching of identified features of an image over time. It is probable that second-order stimuli contain identifiable, low-level features, e.g., regions of high contrast, that can be matched (Anstis, 1980; Braddick, 1980) or attentively tracked (Cavanagh, 1992). Ullman's (1979) 'minimal mapping theory' provides algorithms for computing probable correspondences between the 'matched' or 'tracked' features that are detected at different times. These strategies are considered to be mediated by higher-level mechanisms which do not use low-level, energy-based operations to detect motion.

Correspondence-based models provide theoretically capable mechanisms of second-order motion detection. However, the substantial psychophysical evidence involving low-level mechanisms in motion detection of both types favours models which use, at least at some point, motion energy information contained in the image.

Energy-based models explain second-order motion detection in terms of low-level, passive mechanisms. These models fall into two broad classes. The first class of models suggests that first- and second-order motion are detected by a common low-level

mechanism, exemplified by the spatiotemporal gradient model of Johnston et al. (1992) and that of Grzywacz (1992), whose model detects both motion types by spatiotemporal filtering followed by rectification of motion signals and motion energy detection. The second class of models suggests that first- and second-order motion processing is carried out at least initially, by separate low-level mechanisms but which operate in parallel using qualitatively similar principles of detection. Chubb and Sperling (1988) have shown that theoretically, non-linear processing (e.g., such as rectification or response squaring) of the luminance profile of a second-order stimulus results in the production of luminance components in the image able to be processed by conventional, low-level detectors.

Using this second conceptualization, Wilson et al. (1992) proposed a model of two-dimensional motion processing consisting of two parallel, low-level motion detection pathways, the outputs of which are integrated at a higher level. In one pathway, first-order or 'Fourier' motion energy is detected by a spatiotemporal filtering stage (presumably RFs of V1 neurons) which is then followed by conventional, linear motion energy computation. The second is a 'non-Fourier' pathway which includes a non-linear transformation (e.g., rectification) of the luminance profile of 'non-Fourier' information. The rectified signals can then be detected conventionally by a second stage of filtering at a different orientation and lower spatial frequency. Wilson et al. (1992) suggest that the second filtering stage could be located at V2, which contains cells responsive to non-luminance defined motion; e.g., illusory contours (von der Heydt & Peterhans, 1984). The 'Fourier' and 'non-Fourier' signals are then integrated at a final processing stage, presumably at the medial temporal (MT) area (e.g., Movshon et al., 1986) (see Figure 4).

Wilson et al.'s (1992) model for two-dimensional motion perception is arguably the most complete and influential second-order motion processing model currently available, due in part to its incorporation of both psychophysical and physiological considerations regarding the processing of both motion types. Furthermore, this model has the additional feature of being able to predict the direction of moving type II plaid patterns across a

number of motion parameters (Mather & West, 1993), providing additional evidence that first- and second-order motion are initially processed by independent, low-level mechanisms before ultimately being integrated at a higher level (e.g., Chubb & Sperling, 1988; Wilson et al., 1992; Nishida & Sato, 1995; Nishida et al., 1997b).

In relation to the MAE literature, it has been suggested that the sMAE reflects adaptation of the low-level motion mechanisms prior to first- and second-order signal integration, whereas dMAE may be the result of adaptation at or after the stage of integration (Nishida & Sato, 1995) (see Figure 4).

Second-Order Motion Processing Across the Visual Field

In recent years, a number of psychophysical studies, such as the ones cited in previous sections, have investigated the properties of second-order motion. The findings from these studies have led to better definitions of second-order motion characteristics across a variety of experimental conditions, the results of which have been essential in the development of several comprehensive models regarding the processing of this motion type. However, the vast majority of second-order studies have used central presentation procedures and therefore, the defining characteristics and models have been based on findings selective to central processing mechanisms of second-order motion. In order to fully understand or at the least theorize about how second-order motion is processed, it is useful to know whether or not these defining characteristics are constant as a function of visual field presentation or whether second-order motion processing is exclusive to central vision.

At the present, there are relatively few systematic investigations of second-order motion characteristics of peripheral vision. However, one second-order motion property that has been investigated has been its motion sensitivity across the visual field. These

High-level
motion system

Area MT

Motion integration

Accessed by
Dynamic Test
(dMAE) Only

Motion detection

Area V2

Rectification

Low-level
motion system

Area V1

Accessed by
Static (sMAE)
and Dynamic
Tests (dMAE)

Motion detection

Second-order or
non-Fourier Pathway

First-order or
Fourier Pathway
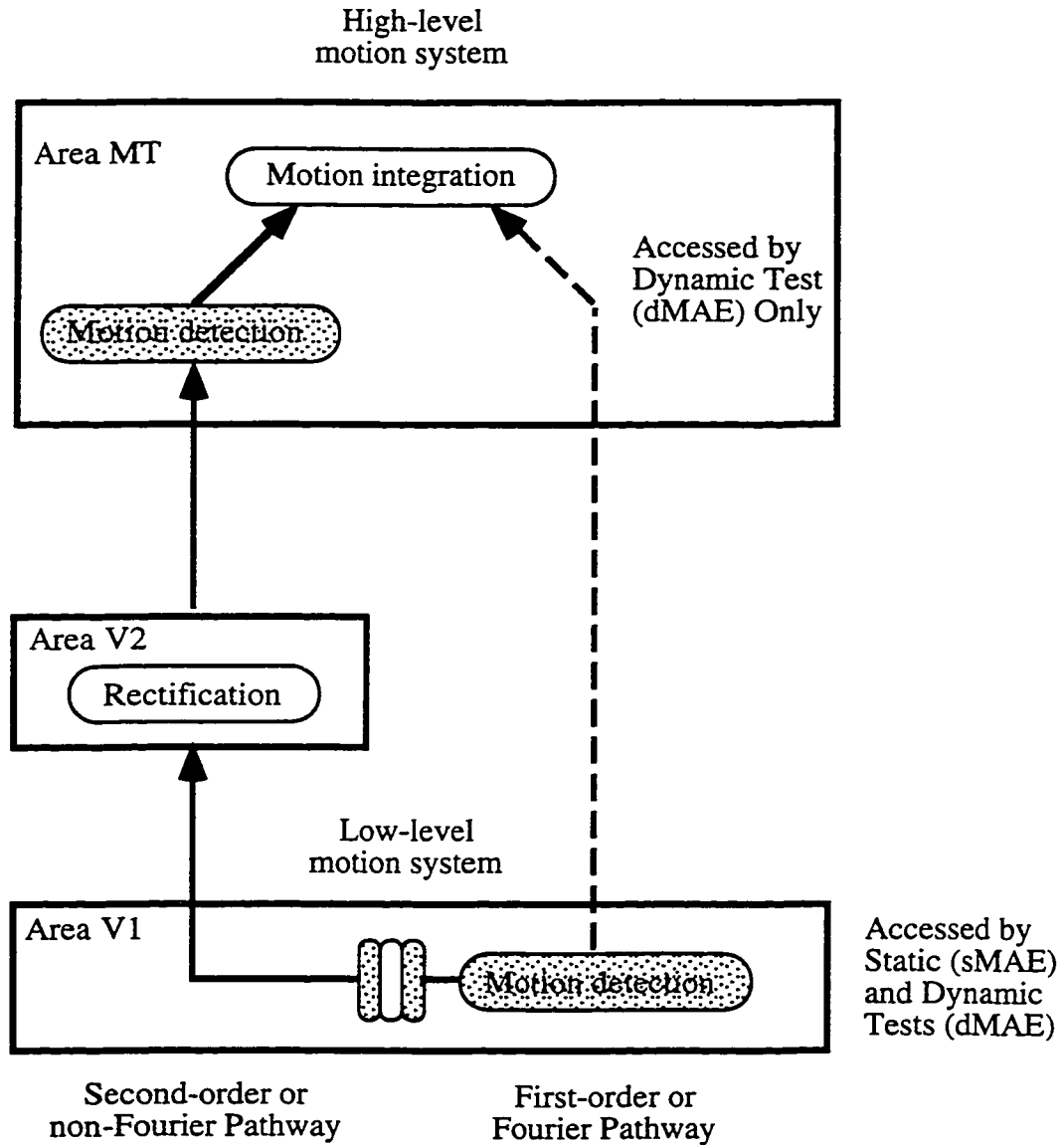
Figure 4. Schematic representation of Wilson et al. (1992) hypothetical model.

sensitivity studies have provided valuable comparative information regarding underlying mechanisms of first- and second-order motion detection for both central and peripheral vision. By measuring the rate of sensitivity loss as a function of eccentricity for both motion-types, inferences can be drawn regarding whether or not similar motion detecting mechanisms are operating on both types of motion across eccentricity.

Motion Sensitivity Studies

Pantle (1992) investigated the motion sensitivity of a second-order stimulus in the peripheral visual field using direction- and orientation-identification tasks. He found that under a broad set of viewing conditions, the motion of a variety of second-order patterns appeared static to the observers when presented in the periphery (8 deg), although their orientation was visible. Similar results were found using flicker-defined second-order patterns (McCarthy et al., 1994; Zanker, 1997). Based on these results, it was suggested that second-order motion detection is a process mediated by mechanisms which operate in central vision only. Other studies, however, have shown that the detection of first- and second-order motion have similar properties in both central and peripheral visual fields.

Smith et al. (1994) measured direction identification thresholds for both first- and second-order motion across a range of eccentricities. Using contrast modulated static noise as a second-order pattern, these researchers found that second-order motion was indeed visible in the periphery (see also Solomon & Sperling, 1995), detectable up to at least 20 deg. They attributed the 'immobility' of second-order stimuli in Pantle's study to the low drift-rate of his second-order patterns, which were tested at only one eccentricity (8 deg). Furthermore, they found that the direction-identification thresholds for second-order motion declined at a similar rate when compared to those of first-order motion. The lack of any qualitative differences between first- and second-order sensitivity were interpreted as being the result of their detection being mediated by mechanisms operating on similar principles, in both central and peripheral visual fields.

The findings of Smith et al. (1994) were questioned by Smith and Ledgeway (1998) on the basis of the type of second-order stimulus that was used. They argued that contrast modulated static noise may not be an appropriate second-order pattern because it may contain first-order artifacts (see Smith & Ledgeway, 1997). The detection thresholds using the 'contaminated' second-order patterns may therefore be in part based on the first-order artifacts presumably present within the pattern and not on the second-order property of the pattern itself. In order to rectify this possible confound, Smith and Ledgeway (1998) used theoretically equivalent contrast modulated dynamic noise patterns as second-order stimuli in their experiment, which they argued to be a true second-order stimulus accessible to only the second-order motion system. Using both static and dynamic second-order patterns, Smith and Ledgeway (1998) reported that although the direction-identification thresholds for the dynamic patterns were significantly elevated across eccentricity compared to the static patterns, the rate of sensitivity decline was nonetheless similar to those of first-order motion. These results, in line with those of Smith et al. (1994), suggest that at least for motion sensitivity, the two motion types seem to share similar properties in both central and peripheral regions.

The conflicting findings of the aforementioned sensitivity studies could be attributable to several factors, as mentioned in the Smith et al. (1994) study. Based on the findings of the sensitivity studies, the question as to whether the second-order motion and its underlying mechanisms are exclusive to central vision is somewhat unresolved.

Overview of the Present Study

Purpose of the Present Study

As reflected in the selective review in previous sections of this dissertation, MAE properties of both first- and second-order motion in central vision has been investigated

extensively (see Culham, 1998). Models of first- and second-order motion processing have been proposed based on adaptation studies using a variety of adaptation and test parameters, the results of which have enabled us to define the properties of the two motion types and the probable sites of their underlying mechanisms along the motion pathway. Although several studies have investigated MAE properties of first-order motion in the periphery (e.g., Wright & Johnston, 1985; Wright, 1986), second-order characteristics have not yet been investigated. As a result, the question of whether second-order motion MAE properties are similar in central and peripheral vision has not been addressed.

The purpose of the present study is therefore two-fold. Firstly, to define the MAE properties of second-order motion across eccentricity using both static and dynamic test patterns of both first- and second-order types. Secondly, to compare the second-order MAE properties with those of first-order across eccentricity, the results of which will be used to address the question whether or not the second-order motion characteristics and its underlying mechanisms are exclusive to central vision. Differences in static and dynamic MAE durations between central and peripheral presentations suggest that current second-order motion models may not apply to peripheral second-order motion processing.

Preliminary Experiments

Two preliminary experiments (Experiment 1 & 2) were conducted before the main adaptation experiment. The purpose of the preliminary experiments was to approximate the suprathreshold visibility between the first- and second-order stimuli across eccentricity for each observer. In Experiment 1, motion sensitivities were determined for both motion types by finding their direction-identification thresholds as a function of eccentricity. The second-order motion visibility was then equated across eccentricity by scaling the second-order direction-identification thresholds (e.g., 100 % modulation at largest eccentricity). Although the first-order thresholds were not used in equating visibility, they were

nonetheless measured to compare the differences in sensitivities between first-and second-order stimuli used in the present experiment to those found in previous studies.

The purpose of Experiment 2 was to approximately equate the visibility of first- and second-order motion at each eccentricity for each observer. The modulation depths of the first-order stimuli were found by subjectively matching them to the scaled second-order stimuli at each eccentricity. The stimuli were matched using a PESTing (parameter estimation by sequential testing) procedure rather than the more conventional method of multiples of direction-identification threshold in order to avoid large differences in relative visibility between each motion type across eccentricity. By using the multiple of threshold method, it is assumed that the relationship between first-and second-order visibility is constant across eccentricity. It is also assumed that the suprathreshold appearance changes in similar ways for both stimulus types. There is, however, no evidence that this is true. These assumptions were avoided by PESTing each first- / second-order pair at each eccentricity individually.

Although the main purpose of the preliminary experiments was to equate the stimulus attributes across eccentricity for the main study for each observer, the methods and results obtained in Experiment 1 & 2 will be presented and discussed in full because they provide additional information regarding the properties of the two motion mechanisms.

Main Experiment

The main experiment (Experiment 3) was designed to examine the MAE properties of first- and second-order motion across eccentricity. Adaptation stimuli consisted of either first- (luminance-modulated noise) or second-order (contrast-modulated noise) drifting patterns which were equated for visibility at each of the four visual eccentricities (0, 4, 8 and 12 deg). The durations of both static and dynamic MAEs were measured to evaluate the different processing levels of each motion type in both the central and peripheral visual

fields. Test stimuli included static and dynamic versions of both motion types (e.g., a static first-order test pattern and a dynamic first-order test pattern) in order to evaluate any cross-adaptation effects. The static tests were simply stationary versions of the adapting patterns whereas the dynamic tests were constructed by successively phase shifting static patterns by 180 deg, resulting in an ambiguous, counterphasing dynamic test pattern.

Because first- and second-order patterns were approximately equated for both visibility and noise at each eccentricity, there is no apriori reason to expect qualitatively different MAE characteristics between the two motion types in the periphery compared to their well defined central properties. Static MAEs are expected after adaptation to first-order motion only, with durations increasing with eccentricity because the patterns are not scaled for size or spatial frequency (e.g., Wright, 1986). Dynamic MAEs, however, are expected after both first- and second-order adaptation at each eccentricity. Since MAE properties of second-order motion have yet to be investigated in the periphery, the question of whether second-order motion properties are exclusive to central vision has not been addressed. If qualitatively different MAE properties are found in the periphery, it can be argued that present models of first- and second-order motion, based in part on results of central MAE studies, may be specific to central vision.

EXPERIMENT 1

Direction-Identification Thresholds for First- and

Second-Order Motion in the Central and Peripheral Visual Field

The primary purpose of this preliminary experiment was to equate the suprathreshold visibility of the second-order patterns across eccentricity. In order to do so, the direction-identification thresholds of the second-order motion were found at each eccentricity and then multiplied by a common multiple. Although they were not needed for scaling, the direction-identification thresholds of first-order patterns were also found in order to compare them to those of second-order at each eccentricity.

As mentioned in the Introduction, motion sensitivity studies have provided a method for comparing first- and second-order motion processing across eccentricity, at least for motion detection. It has been argued that if motion sensitivity declines with eccentricity at a similar rate for first- and second-order motion, then the two motion types are detected by common underlying mechanisms or with separate mechanisms having similar properties (Smith et al., 1994). Studies using second-order stimuli defined by contrast modulated noise (similar to the stimuli used in the present study) have found a similar rate of sensitivity decline for the two types of motion, whether the second-order carrier is static (Smith et al., 1994) or dynamic (Smith & Ledgeway, 1998). Using the direction-identification thresholds found in this first preliminary experiment, motion sensitivities were calculated for both motion types across eccentricity in order to see if these results were generalizable to the stimuli used in the present study. Based on previous findings, it is therefore expected that (1) both first- and second-order sensitivities will decrease with eccentricity and (2) the sensitivity of the two motion types will decrease at approximately the same rate.

Method

Participants

Four psychophysically experienced observers (2 males and 2 females) participated in all conditions of the study. All observers had previous experience in psychophysical experiments but only two (AB and MvG) were familiar with MAE experiments. All observers had normal or corrected-to-normal vision. Those who wore corrective eyeglasses wore them throughout experimentation. A fifth observer was omitted from testing after not being able to identify second-order motion direction in the periphery, even at contrasts that were far above threshold for all other observers at each eccentricity.

Apparatus

Stimulus presentation and data collection were controlled by a Power Macintosh 7200/90 microcomputer and presented on a 16-inch AppleVision 1710 monitor with a frame refresh rate of 75 Hz. The screen resolution was 1024 x 768 pixels. Stimulus generation and animation were controlled by the Pixx© program developed by the Concordia Vision Lab (author, Peter April). Color calibration and luminance readings were taken using the Minolta CS - 100 Chroma Meter colorimeter.

Stimuli

Second-order stimulus

The second-order stimulus used for the direction-identification threshold tasks and in all subsequent testing was a contrast-modulated (CM) noise pattern whose luminance profile at point (x, y) was defined by the following equation:

$$L\ (x, y) = L_{mean}\ \{[1 + m_{env} \cdot sin2\pi x f] \cdot [1 + 0.5\ m_{car} \cdot R(x, y)]\}$$

where L_{mean} is the mean luminance of the display (32.30 cd/m^2), m_{env} and f are the modulation depth and the spatial frequency of the envelope, respectively, and m_{car} is the contrast of the carrier. $R(x, y)$ is the carrier made of static noise consisting of dots (1 pixel x 1 pixel, measuring approximately 2.235 arc min) whose individual luminances were randomly assigned as a function of sin(x), where (x) ranged from 0 to 2π. This sinusoidal modulation resulted in a static carrier which was greyscale in nature. The carrier was modulated by multiplying it to a vertically oriented sinewave grating (envelope) with a spatial frequency of 0.5 cycles per degree (c/deg), drifting horizontally either to the left or right at 2 cycles per second (Hz). The envelope was kept fully modulated ($m_{env} = 1$) throughout experimentation. The maximum contrast in the carrier (m_{env}) of second-order patterns was modulated and could be varied within a range of 0.0 and 1.0 defined as:

$$\text{luminance modulation depth} = (L_{max} - L_{min}) / (L_{max} + L_{min})$$

where L_{max} and L_{min} are the maximum and minimum adjacent pixels with opposite polarity in the high contrast region of the carrier. A grey field of mean luminance (L_{mean}) resulted when the carrier contrast was zero.

First-order stimulus

The first-order stimulus was a luminance-modulated (LM) noise pattern produced by adding rather than multiplying the same static greyscale carrier to a modulating sinewave grating. LM noise patterns were used as the first-order stimuli instead of more conventional sine wave gratings in order to keep the first- and second-order stimuli as perceptually similar as possible. The amplitude of the luminance modulation (m_{env}) for the first-order patterns could be varied from 0.0 to 0.5 defined as:

$$\text{luminance modulation depth} = (L_{max} - L_{min}) / (L_{max} + L_{min})$$

where L_{max} and L_{min} are the maximum and minimum mean luminances averaged over pairs of adjacent pixels with opposite polarity.

Display

Eccentric presentations for this and subsequent experiments were created by displacing the fixation spot (0.35 x 0.35 deg) along the vertical midline of the display at 0 (foveal) , 4, 8 or 12 deg from the center of the moving pattern. As shown in Figure 5, first- and second-order patterns were always presented within a stimulus window fixed at the lower portion of the display which subtended 2 deg vertically and 8.5 deg horizontally and was viewed from a distance of 57 cm. This defined the size of all the patterns throughout all experimental sessions.

The mean luminance of the rest of the display was 32.30 cd/m^2 (u'= .1832, v'= .4608 in CIE (Commission Internationale de l'Eclairage) u'v' colour space) where L_{min} and L_{max} were 0.19 & 64.60 cd/m^2, respectively. Eccentric fixation was used in order to minimize any global distortion products that may have been present as a results of spatial nonlinearities of the CRT (cathode ray tube) display used in this study (see *Global and Local First-Order Artifacts*). A residual benefit of this type of presentation was that no part of the patterns ever fell into the blind spot of either eye.

Global and Local First-Order Artifacts

Recently, a number of studies investigating second-order motion properties have been conducted using contrast-modulated noise patterns (e.g., Smith et al., 1994; Solomon & Sperling, 1995; Smith & Ledgeway, 1998). Smith and Ledgeway (1997) have argued that this type of stimulus, particularly those constructed with static carriers, may not be 'pure'
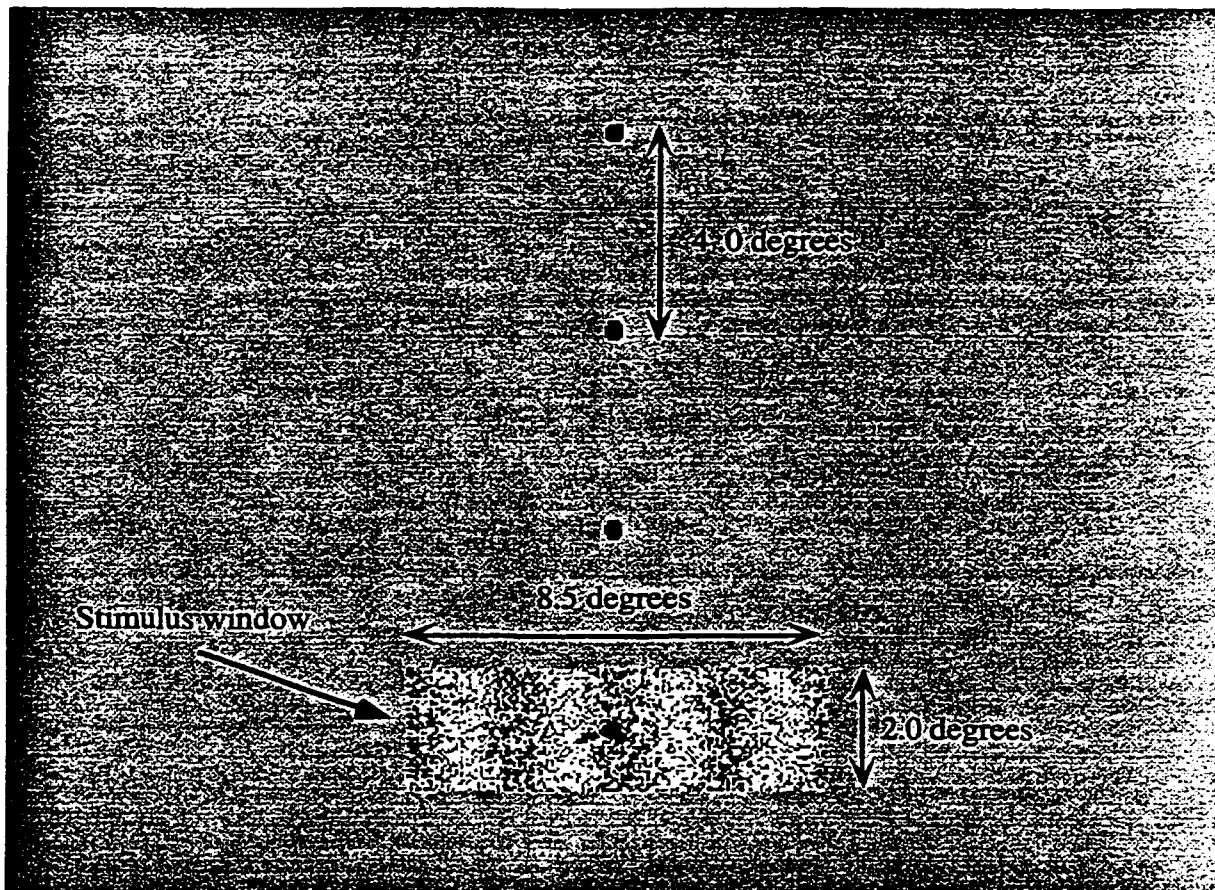
Figue 5. Display setup used throughout experimentation.

second-order stimuli because first-order artifacts may be present in the second-order patterns. They argue, therefore, that the motion detection of contrast-modulated patterns may reflect the detection of first-order motion from the luminance artifacts present in the assumed second-order stimuli. Two potential sources of luminance artifacts (global and local artifacts) will be described as well as how they were minimized in the present study.

Global Artifacts

The first potential source of artifacts is known as global distortion products and arise in the image presented on the monitor or CRT display (Brown, 1995; Naiman, 1991; Naiman & Makous, 1992). Basically, the relationship between the voltage output (DAC values) and measured luminance is non-linear, with the result that a DAC step (Δx) at low luminance values is physically less than the same DAC step at higher luminance values. This non-linearity results in unwanted luminance artifacts in the second-order patterns because globally, the carrier is brighter than it should be. When modulated with a moving sinewave, a first-order modulation is introduced because the luminance of the carrier varies across space in a way that is not symmetrical relative to the mean luminance of the pattern. To minimize any global distortion products, and therefore to eliminate any first-order artifacts in the second-order stimuli, the voltage-luminance nonlinearity of the monitor was gamma-corrected (linearizing the voltage-luminance relationship) by colour calibrating the monitor. Gamma-correction was implemented with a calibration within the Pixx program, the software used to produce the stimuli.

As an additional precaution against possible global luminance artifacts, both first- and second-order patterns throughout experimentation were always presented at the same display location (within the stimulus window). Eccentric presentations were therefore produced by moving the fixation spot relative to the spatially fixed patterns. This procedure was adopted because the luminance of CRT displays is characteristically non-homogenous (Mulligan & Stone, 1989; Naiman & Makous, 1992). By presenting the second-order patterns at different spatial display locations, unwanted luminance distortions

might have been introduced in the second-order patterns because the luminance values of the calibrated stimuli might have varied if the spatial location of the pattern was moved across the non-homogenous display.

Local Artifacts

The second type of luminance artifact has been argued to occur even when global artifacts are minimized. Theoretically, the luminance of a second-order carrier should vary across space in a manner which is symmetrical, or drift balanced (Chubb & Sperling, 1988) about the mean luminance. Smith and Ledgeway (1997) argue that both binary and greyscale carriers contain local areas where the proportion of light and dark pixels is not balanced or equal. Basically, if the carrier contains a local area where a cluster of either light or dark pixels predominates, a local luminance imbalance occurs. When multiplied with a drifting sinewave, the luminance imbalances create local first-order artifacts in the direction of the modulation and therefore, the moving contrast-pattern will be luminance defined and not completely second-order. Smith and Ledgeway (1997) suggest that the use of a dynamic noise carrier and small noise (pixel) sizes reduce the possibility of local first-order artifacts in the second-order stimuli.

It can be argued, however, that the local artifacts that might exist are simply too small to potentially be used by the observers (e.g., Benton & Johnston, 1998; Sperling & Lu, 1998), especially in the periphery where spatial resolution is relatively coarse. Nonetheless, the smallest possible pixel size was used to create the carrier, a precaution which undoubtedly minimized any potential luminance artifacts in the second-order patterns.

Procedure

The participants were tested individually in a dark laboratory room, the only source of illumination being the display itself. Procedural interactions were given verbally to the

participants before each experimental session. Participants viewed the display binocularly from a distance of 57 cm for all conditions. Head movements were minimized using a head and chin rest.

A typical experimental session consisted of presentations of first- and second-order patterns drifting either to the left or right at each of the four (0, 4, 8 or 12 deg) eccentricities. All possible combinations were presented randomly. A session ended when direction-identification thresholds were found for all eight (motion type X eccentricity) experimental conditions.

Observers initiated each trial by pressing the space-bar on the keyboard. A fixation spot was presented at one of the four eccentricities, allowing the observers to foveate on the fixation point. Two seconds later a first- or second-order pattern moving to the left or right was presented in the stimulus window. The moving patterns were presented for two seconds. The observers' task was to identify the direction of the presented drifting pattern by means of a two-alternative, forced-choice (2AFC) method. The '0' key on the numeric keypad was depressed if a 'left' judgment was made and the '. (period)' key was depressed for a 'right' judgment. Because eccentric fixation was used, participants were told that the location of the fixation point would change from trial to trial along the vertical line centered on the display. For this reason, they were reminded of the importance of keeping continuous fixation on the spot throughout all trials

Direction-identification thresholds for first- and second-order motion across eccentricity were determined using a 'Best PEST' (parameter estimation by sequential testing) (Pentland, 1980) routine, an improved version of the original PEST procedure introduced by Taylor & Creelman (1967). This method was chosen over the more conventional staircase procedures because the PEST has been shown to significantly reduce the number of trials necessary to determine a threshold compared to staircase methods at a given level of accuracy (Lieberman & Pentland, 1982).

For the SO patterns, thresholds were measured in terms of amount of luminance contrast needed in the high contrast region of the carrier in order to make a direction discrimination. For FO patterns, the luminance modulation was the physical variable being manipulated during the PEST sessions. A session ended when the PEST routine converged on the 81 % level on a Weibull (Weibull, 1951) function (thresholds at which observers were able to discriminate the correct direction of the pattern 81 % of the time) for all eight (motion-type x eccentricity) conditions. A preset level of accuracy (95% confidence interval hat the true threshold was within 0.1 log units of the PESTed threshold) had to be met in order for the PEST routine to end for each condition. Maximum number of trials was fixed at one-hundred for each condition. If the level of accuracy wasn't met for any condition (e.g., not before 100 trials), the threshold obtained at the hundredth trial was used. Each 'PEST' session took between 35 and 45 minutes. Observers were tested three times to obtain an average direction-identification threshold for each condition.

The second-order thresholds were used to scale the visibility of second-order patterns across eccentricity. This was done by maximally modulating (100 %) the second-order patterns at the eccentricity with the highest direction-identification threshold, which in the present study, was always at the highest eccentricity (12 deg). The thresholds at the other eccentricities were then set to the same multiple of direction-identification threshold, resulting in second-order patterns which were equated for suprathreshold visibility across eccentricity.

Results

The raw data consisted of each observer's mean direction-identification thresholds (measured in percent modulation) for each motion type at each eccentricity found using the PEST procedure. Mean thresholds (averaged over three trials) for all conditions are shown in Table 1 for all observers. Also shown in Table 1 are the scaled second-order modulation depths (SO*) for each observer.

An analysis of variance (ANOVA) (Appendix A, Table 1 & 2) was performed on the threshold data to examine the change in threshold of both motion types as a function of eccentricity. When averaged across observers, it was found that the direction identification thresholds significantly increased with eccentricity for both first- [$F(3,9)=10.272$, $p<.05$] and second-order patterns [$F(3,9)=14.922$, $p<.05$], as shown in Figure 6a and b, respectively.

In order to compare the relative rate at which motion sensitivity declines as a function of eccentricity for the two motion types thresholds were normalized by expressing them in terms of relative sensitivity (dB), where the sensitivity at each eccentricity for each motion type was calculated relative to the highest sensitivity (or lowest threshold), which was usually found at foveal presentations for all observers. By measuring the relative sensitivity, the relative rate of sensitivity decline can be measured independently of differences in absolute sensitivities between the two motion types, as shown in Figure 7. By definition, most of the foveal sensitivities (dB) were zero because for all but one observer, both first- and second-order direction-identification thresholds were found to be lowest when presented foveally. This resulted in variance heterogeneity among the treatment means because the variance of the motion sensitivity values at foveal presentations was much smaller than those found at the other eccentricities. In an attempt to correct for the variance inhomogeneity, a more stringent alpha value of 0.025 was used to evaluate the F ratios. As expected, a two-factor ANOVA (Appendix A, Table 3)

Table 1

Threshold modulation depths for first-order (FO) and second-order (SO) motion at each eccentricity and scaled SO modulation depths (SO*) across eccentricity for all four observers.

Eccentricity	0 degrees			4 degrees			8 degrees			12 degrees		
Motion Type	FO	SO	SO*	FO	SO	SO*	FO	SO	SO*	FO	SO	SO*
AB	0.44	8.91	19.81	0.77	21.34	47.43	0.67	39.96	88.81	1.00	45.00	100.0
MvG	0.43	16.01	27.72	0.57	38.63	66.90	0.82	50.59	87.61	1.02	57.74	100.0
MI	0.73	7.32	19.30	0.73	15.28	40.26	0.83	35.52	93.62	1.08	37.95	100.0
CV	0.47	7.03	37.45	0.57	12.72	67.81	0.68	11.52	61.37	0.65	18.76	100.0

Note. All thresholds expressed in % modulataion. Thresholds ir each cell an average from three trials.
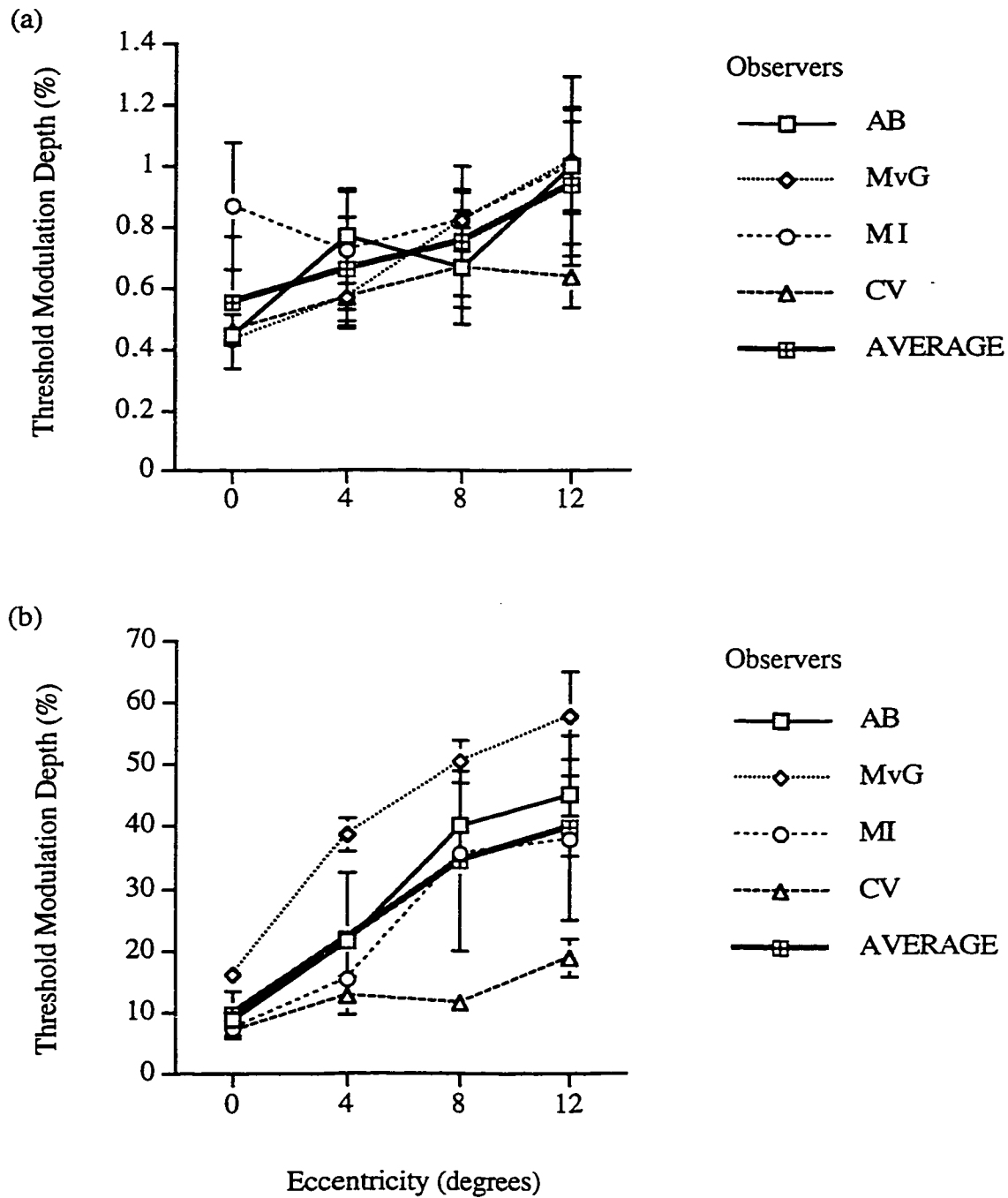
Figure 6. Direction-identification thresholds for (a) first- and (b) second-order patterns as a function of eccentricity for each observer. Each point represents the average of three thresholds.
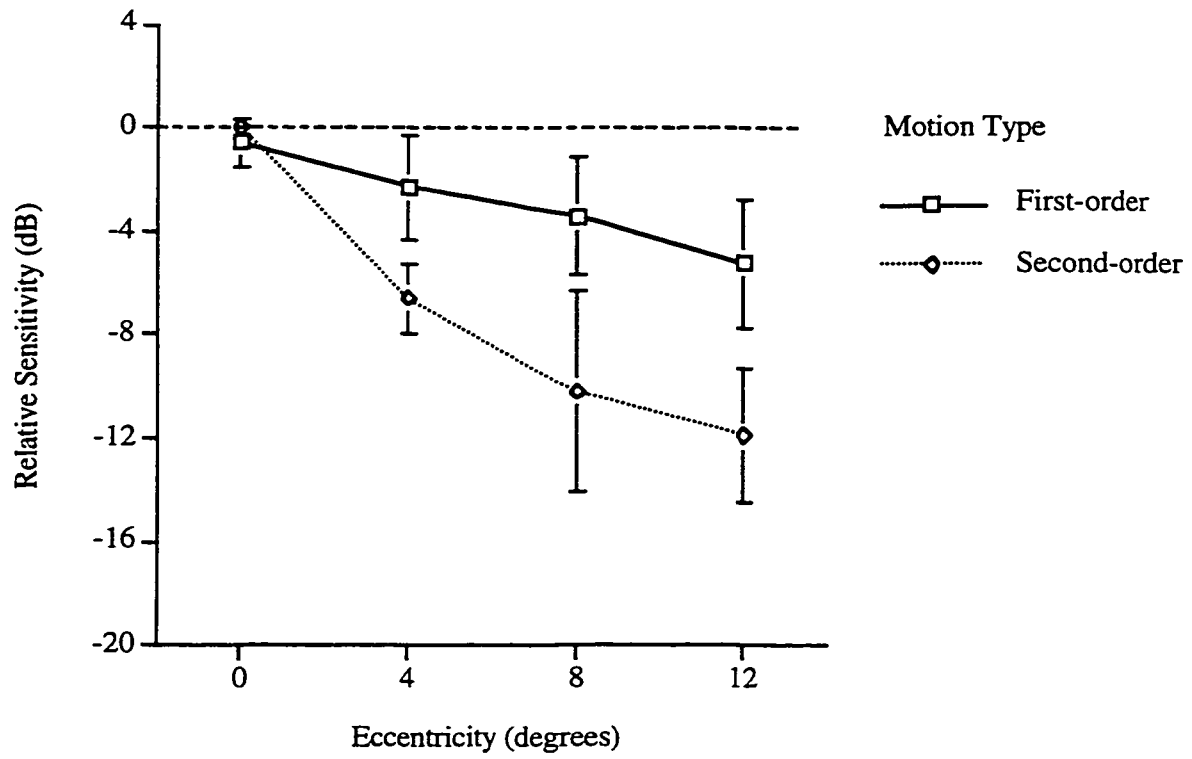
Figure 7. Sensitivity functions derived from direction-identification

thresholds of each motion type expressed in relative sensitivity (dB).

revealed a significant decline in sensitivity across eccentricity when averaged across both motion types [$F_{(3,9)}=42.981$, $p<.025$]. However, when averaged across eccentricity, motion sensitivity was higher for first-order motion compared to that of second-order motion [$F=(1,3)=16.997$, $p<.025$]. Furthermore, a significant Motion Type x Eccentricity interaction effect was also found [$F_{(3,9)}=6.303$, $p<.025$], suggesting that the sensitivity of second-order motion decreased with eccentricity at a significantly steeper rate compared to that of first-order motion.

Discussion

The results partially support the initial hypotheses. As expected, motion-identification thresholds increase with eccentricity for both first- and second-order motion. Also, the direction of second-order motion is detectable at least to 12 degrees eccentricity, a finding at odds with those of Pantle (1992) who reported that the motion of a variety of second-order patterns is not visible in the periphery (8 deg). However, the sensitivity of the two motion types did not decrease at the same rate, as was expected. Motion sensitivity to second-order motion decreased at a significantly faster rate than that of first-order motion. This result differs from those of Smith et al. (1994) and Smith and Ledgeway (1998), who found a similar rate of motion sensitivity decline for both motion types, even when the second-order stimuli were constructed using a dynamic carrier (Smith & Ledgeway, 1998).

Smith et al. (1994) investigated motion sensitivity of the two motion types at up to 20 degrees of eccentricity. They concluded that the rates are similar for the two motion types, reaching approximately the same attenuation (in dB) at 20 degrees for both observers. Although this appears to be true, the difference between first- and second-order rates of sensitivity decline from 0 to approximately 12.5 degrees in their study appears quite comparable to the one found in the present study. The first-order sensitivity seems to be decreasing linearly and at a slower rate compared to that of second-order sensitivity, which in both cases has a much steeper rate of decline between 0 and 12.5 degrees. The second-order rates are similar, however, beyond 12.5 degrees where they appear to level off (flatten) and eventually equal the first-order rates at around 20 degrees. However, Smith et al. (1994) conclude that the rate of sensitivity loss is similar for both motion types at all eccentricities, a conclusion which is debatable because their data and the present sensitivity data share two common characteristics. Firstly, second-order sensitivity was always less than first-order sensitivity across all eccentricities. Secondly, the second-order

sensitivity appeared to decrease more quickly, defined by an initial steeper rate of decline in sensitivity, especially from 0 to 8 degrees of eccentricity.

Smith and Ledgeway (1998) also reported that sensitivity declines with eccentricity at a similar rate for first- and second-order motion when using either static or dynamic carriers in the second-order patterns. Although their results were not replicated, it can be argued that using a static noise carrier, as was the case in the present study, does not seem to lead to local first-order artifacts in the second-order pattern because the second-order sensitivity in the present study declined at a faster rate than that of the first-order. If the presence of local first-order artifacts did mediate the detection of the second-order patterns, it might be expected that the rate of second-order sensitivity decline would be more similar to that of first-order stimuli, i. e., decline at a slower rate.

In conclusion, the finding that the motion sensitivities of first- and second-order motion fall off with eccentricity at dissimilar rates can be interpreted as being the result of their respective mechanisms operating on different principles in central and peripheral fields of vision, at least for mechanisms mediating the detection of their motion.

EXPERIMENT 2

Visibility Matching of First-and Second-Order Stimuli Across Eccentricity

The primary purpose of the second preliminary experiment was to approximately equate the suprathreshold visibility between first- and second-order motion patterns at each eccentricity. Equating the visibility between first- and second-order stimuli is an important procedure since performance on a psychophysical task often varies with degree of stimulus contrast. As mentioned in the Introduction, MAE duration varies with adaptation and test stimulus contrast (e.g., Keck et al., 1976; Nishida et al., 1997). Because the visual system is differentially sensitive to first- and second-order patterns, it is important to equate the visibility of these two motion types if valid comparisons and conclusions are to be made between these stimulus. This is especially true in this study where the matched first- and second-order patterns will be used as adaptation and test patterns in the main experiment (Experiment 3) which investigates the MAEs resulting from adaptation to both motion-types.

When equating for visibility within a class of stimuli defined by a characteristic property (e.g., luminance-defined), it is possible to physically equate the stimuli using psychophysically defined criteria, such as multiples of the direction-identification threshold. This procedure was used in Experiment 1 to equate the visibility of the second-order patterns across eccentricity. It is less obvious, however, to physically equate the visibility between stimulus classes (e.g., between first- and second-order patterns). One method that is commonly used to equate the visibility of first- and second-order patterns is by setting the modulation depths of the patterns at equal multiples of their respective direction-identification thresholds. Studies using this method of equating the visibility of first- and second-order patterns have shown that foveal velocity discrimination (Turano & Pantle, 1989) and MAE duration (Ledgeway & Smith, 1994b) are qualitatively the same for the first- and second-order patterns. Although this equating method may be appropriate for

central presentation, it may be impossible to use this method to equate between first- and second-order stimuli across eccentricity, especially since the suprathreshold visibilities are derived from direction-identification thresholds, which at least in the present study (Experiment 1), do not seem to vary across eccentricity in a similar manner for the two motion types.

The present study therefore used a more subjective method in an attempt to approximately equate the visibility between first- and second-order patterns at each eccentricity. The observers were asked to subjectively match the motion saliency between the scaled second-order patterns (found in Experiment 1) and first-order patterns presented at the same eccentricity.

Method

Participants

The same four observers (AB, MvG, MI and CV) who participated in Experiment 1 were used.

Apparatus

The apparatus was identical to that used in Experiment 1.

Stimuli

Second-order stimulus

The second-order patterns used in the matching task were the scaled second-order patterns (SO*) found in Experiment 1 for each observer at each eccentricity (see Table 1). The suprathreshold visibility of these patterns was kept fixed throughout experimentation because they served as the 'reference' patterns at each eccentricity. Both second- and first-order patterns were otherwise identical to those used in Experiment 1.

First-order stimulus

The first-order patterns were 'matched' to the scaled second-order patterns (SO*) at each eccentricity. Their modulation depths were therefore varied between 0.0 and 0.5 according to the observers' responses.

<u>Procedure</u>

The experimental setup was identical to that of Experiment 1. A typical experimental session consisted of trials of sequential presentations of scaled second-order patterns (SO*) (or 'reference' patterns) and first-order patterns (or 'match' pattern) at the same eccentricity. 'Reference-match' dyads were randomly presented at each eccentricity and both patterns moved in the same direction (either to the left or right) in each trial. Sequence of presentation was also randomized, i.e. it was either 'reference'-'match' or 'match'-'reference'. A session ended when 'matching' modulation depths were found for the first-order patterns at each of the eccentricities for both left and right directions.

Observers initiated each trial by pressing the space-bar on the keyboard. As in Experiment 1, a fixation spot was presented at one of the four eccentricities for two seconds allowing the observers to fixate prior to the presentation of the patterns. After two seconds, a 'reference'-'match' dyad, with both patterns moving either to the left or to the right, was presented in the stimulus window. Each pattern within the dyad was presented for two seconds. The observer's task was to identify which of the two drifting patterns appeared to be more visible using a 2AFC method. The '1' key was depressed if the motion of the pattern presented first in the sequence (whether if be the 'reference' or 'match' pattern) appeared more salient relative to the other and, the '2' key was depressed if the motion of the pattern presented second in the sequence appeared to be more salient.

The 'matching' modulation depth of the first-order patterns was estimated using the same PEST procedure as in Experiment 1. Since the modulation depths of the reference second-order patterns were preset and held constant throughout the matching trials at each eccentricity, the modulation depths of the 'match' (first-order patterns) were varied from trial to trial until the motion of the 'match' pattern was identified as being more salient 81% of the time at each eccentricity for left/right presentations. This resulted in first- and second-order patterns whose motion saliency was just noticeably different (or

for each condition. Each 'PEST' session took between 15 and 25 minutes. Each observer was tested twice to obtain average 'matching' first-order modulation depths at each eccentricity for both motion directions.

Results

The raw data consisted of each observer's mean 'matched' first-order modulation depth (measured in percent modulation) at each eccentricity for both left and right presentations. The left / right modulation depths were collapsed across all conditions, and the resulting first-order mean modulation depths (FO*) gave the matches for the scaled second-order patterns (SO*) at each eccentricity for all observers, as shown in Table 2.

First-order modulation depths were also found across eccentricity using a common multiple of direction-identification threshold, i.e. by multiplying FO direction-identification threshold by SO scaling multiple used in Experiment 1, in order to compare them to the subjectively matched modulation depths (see Figure 8). When averaged across observers, a two-factor ANOVA (see Appendix B, Table 1) revealed that the modulation depths of the subjectively matched FO patterns (FO*) were significantly greater across eccentricity compared to those found using a common multiple of threshold (FO Common) $[F(1,3)=23.847, p<.05]$. Furthermore, the relationship between the 'FO' and 'FO Common' modulation depths were not found to be constant across eccentricity, as evidenced by a significant interaction effect $[F(3,9)=6.277, p<.05]$.

Table 2

Suprathreshold modulation depths of scaled second-order patterns (SO*) and approximately matched first-order (FO*) patterns across eccentricity for all four observers.

Eccentricity	0 degrees		4 degrees		8 degrees		12 degrees	
Motion Type	SO*	FO*	SO*	FO*	SO*	FO*	SO*	FO*
AB	19.81	12.20	47.43	15.30	88.81	23.70	100.0	37.60
MvG	27.72	20.30	66.90	20.50	87.61	26.90	100.0	33.50
MI	19.30	25.20	40.26	27.30	93.62	49.70	100.0	48.90
CV	37.45	13.10	67.81	15.30	61.37	5.40	100.0	29.30

Note. All thresholds expressed in % modulataion. Matched FO* modulation depths an average from two trials.
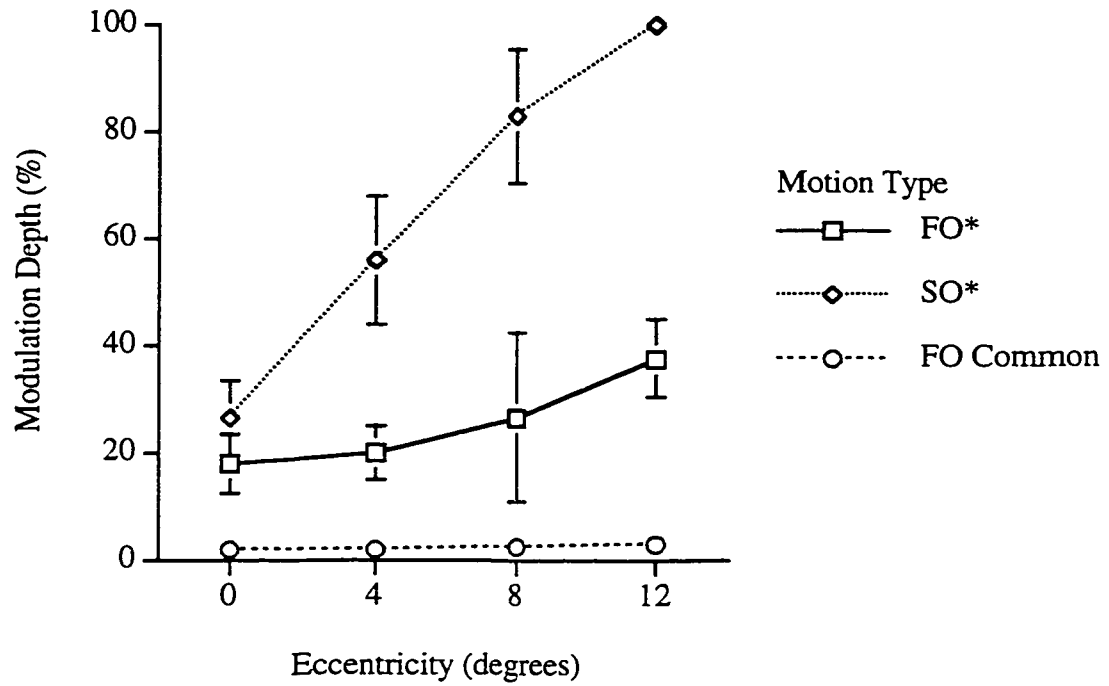
Figure 8. Matched suprathreshold modulation depths between first- and second-order patterns at each eccentricity with modulation depths of first-order patterns set with a common multiple of direction-identification threshold.

Discussion

Many studies investigating different properties between first- and second-order motion in central vision have equated the suprathreshold visibility of the two types of motion by presenting the stimuli at the same multiple of direction-threshold (e.g., Turano & Pantle, 1989; Ledgeway, 1994; Nishida et al., 1997). Although the results from these studies suggest that equating suprathreshold visibility using multiples of the direction-identification threshold may be appropriate for central presentations, the assumption that the same multiple found with central thresholds can be applied to equate first- and second-order patterns in the periphery is unjustified. This assumption was avoided in the present study by subjectively matching the visibility of the first- and second-order patterns at each eccentricity individually, using a method of direct comparison.

The results from Experiment 2 show that the modulation depths (visibility) of the first-order patterns judged by the observers to be approximately equal (FO*) to the second-order patterns at each eccentricity were found to be much greater than those defined by a common direction identification-multiple (FO Common). In addition, it was found that the relationship between the 'FO*' and 'FO Common' modulation depths is not constant across eccentricity. It seems as though a stronger first-order motion modulation was needed in the periphery in order to equate the scaled second-order modulation when compared to the first-order patterns defined by 'FO Common' modulation.

It is evident that the two methods of matching the suprathreshold visibility of first- and second-order patterns result in different relationships between the scaled second-order and respective first-order patterns at each eccentricity. The validity of the subjective matching method used in the present experiment will be empirically tested in Experiment 3. It has been reported that if first- and second-order patterns are equated for both visibility and noise, cross-adaptation between first- and second-order patterns should result in MAEs of similar durations compared to same-adaptation conditions (Ledgeway & Smith, 1994b).

Since the first- and second-order patterns both contain noise, cross-adaptation at each eccentricity should result if the suprathreshold visibility of the first- and second-order patterns were properly matched.

EXPERIMENT 3

Static and Dynamic MAE After First- and

Second-Order Adaptation Across Eccentricity

As mentioned in the final sections of the General Introduction, the MAE properties of both first- and second-order motion are relatively well defined in central vision. The most significant theoretical difference between these two motion-types is their ability to elicit a static MAE (sMAE). Although a robust sMAE is elicited after first-order adaptation, it is now well accepted that a sMAE is not produced after second-order adaptation. This is a test considered to assess the adaptation of conventional, low-level motion mechanisms. However, a clear dMAE is perceived after adaptation to both motion types. These qualitative differences between static and dynamic MAEs elicited after first- and second-order adaptation have been interpreted as evidence favouring different processing sites along the visual pathway for the two motion types. As reviewed in the Introduction, most models of first-and second-order motion processing based on these and other empirical findings have proposed that first- and second-order motion signals are detected, at least initially, by distinct and parallel pathways before being integrated at a higher level (e.g., Wilson et al., 1992; Nishida & Sato, 1995).

These motion models, however, are based on first- and second-order motion properties of central vision. Until the present, there has not been a systematic investigation of second-order motion MAE properties in the periphery, and therefore, it is not known whether or not the defining properties of these two motion types are similar in central and peripheral vision. therfore, the present experiment has two purposes. The first is exploratory in nature since it involves defining the MAE properties of both first- and second-order motion in the periphery. Although some first-order motion MAE properties have been investigated in the periphery, those of second-order motion have not. For this reason, MAE durations after both first- and second-order adaptation were measured using

both static and dynamic tests in order to define the properties of each motion type in both the central and peripheral visual fields. The second purpose of the present study is to compare these central and peripheral MAE properties in order to evaluate whether or not first- and second-order motion share their defining MAE properties across eccentricity.

The visual system's differential sensitivity to first- and second-order motion was controlled for by presenting patterns of both motion types at an approximately equal suprathreshold visibility at each eccentricity, as determined in Experiment 2. Test stimuli included static and dynamic versions of both motion types (e.g., static first- and second-order test pattern) in order to evaluate cross-adaptation effects (Ledgeway & Smith , 1994) across eccentricity. This constitutes another pertinent first- and second-order motion property that has never been investigated in the periphery.

Based on previous findings, it was expected that cross-adaptation effects will occur, at least after central presentations. Since the visibility of first- and second-order patterns were approximated at each eccentricity, it would not be unexpected if cross adaptation effects would be present across eccentricity after adaptation to both motion types. If so, the matching procedure used in Experiment 2 would have to be considered as an appropriate technique for equating suprathreshold visibility between first- and second-order patterns not only in central vision, but also in the periphery.

Based on the findings of Wright (1986), it is expected that the duration of the sMAE will increase with eccentricity after first-order motion adaptation since the patterns were not scaled for size or spatial frequency with eccentricity. A sMAE is not expected after adaptation to second-order motion when presented centrally and there are no apriori reasons to expect sMAEs in the periphery after second-order adaptation. Finally, dMAEs are expected after adaptation to both motion types in both the central and peripheral visual fields.

Method

Participants

The same four observers (AB, MvG, MI and CV) who participated in Experiments 1 and 2 were used.

Apparatus

The apparatus was identical to that used in Experiments 1 and 2.

Stimuli

Adaptation Stimuli

Adaptation stimuli consisted of either first- or second-order drifting grating patterns which were matched for visibility for each individual at each of the four visual eccentricities (0, 4, 8 & 12 deg) according to the results of Experiments 1 and 2.

First-order

The first-order adaptation stimulus was identical to the LM noise pattern used in Experiments 1 & 2 (as described in Experiment 1) and drifted either to the left or right at 2 c/deg at each eccentricity. The luminance modulation depths of the first-order adapting patterns were those of the 'matched' (FO*) modulation depths (see Table 2), found at each eccentricity for each observer in Experiment 2.

Second-order

Similarly, the second-order adaptation stimulus was also identical to the CM pattern used in Experiments 1 & 2. The contrast modulation depth used for the second-order

adaptation patterns was the scaled (SO*) modulation depth (see Table 2), found at each eccentricity for each observer in Experiment 1.

Test Stimuli

For same-adaptation conditions (e.g., adapt with FO pattern and test with FO pattern), the modulation depths of the adapt-test patterns were identical. For cross-adaptation conditions (e.g., adapt with FO pattern and test with SO pattern), the modulation depths of the adapt-test were the ones matched in Experiment 2. Therefore, the contrasts between the adapt and test patterns presented at each eccentricity were always either physically identical (same-adaptation) or subjectively matched (cross-adaptation).

Static

Both first- and second-order static test patterns (referred to as fo st & so st, respectively) were stationary versions of their respective adaptation patterns e.g., static noise carrier either added to or multiplied with the stationary envelope.

Dynamic

First- and second-order dynamic test patterns (referred to as fo dy and so dy, respectively) were produced by phase-shifting stationary frames of either type of motion pattern by 180 degrees, resulting in a directionally-ambiguous, counterphasing test stimulus for each motion type. The stationary frames were phase-shifted every 0.267 sec, resulting in dynamic test which flickered at a rate of 3.75 Hz.

Procedure

The experimental setup was identical to that of Experiments 1 and 2. Procedural instructions were given verbally to the participants before each experimental session. An experimental session consisted of presentations of either first- or second-order adaptation patterns moving either left or right at each of the four eccentricities, replaced by one of the four test patterns (i.e., fo st, fo dy, so st or so dy). A session ended when all sixteen

(adapt drift direction x adaptation type x test type) conditions were presented twice. All possible condition combinations were presented in random order.

Observers initiated each trial by pressing the space-bar on the keyboard after which a fixation spot was presented for two seconds at one of the four eccentricities, allowing enough time for observers to foveate. In each trial, the adaptation pattern (a first- or second-order pattern moving either left or right) was presented for 15 seconds in the stimulus window and was immediately followed by one of the four test patterns. The observer's task was to indicate when the MAE ended by pressing a response button on the keyboard. Therefore, for static tests, a response was made after the pattern ceased to drift in the direction opposite the adapting direction. For the dynamic tests, a response was made as soon as the motion within the test stimulus first appeared to oscillate (or move ambiguously) rather than to move coherently in the direction opposite to adaptation. The observers were instructed to use a consistent response criterion throughout the experiment. If no MAE was perceived, the observers pressed an alternate response button. The test stimulus disappeared as soon as any response was made.

Observers were tested in two separate sessions, resulting in 4 replications of each possible stimulus combination. Each testing session took approximately 75 minutes each to complete.

Results

The raw data consisted of MAE durations after each motion type, measured with each test pattern at each of the four eccentricities. MAE durations for each condition combination were averaged across drift direction (left/right) and session, resulting in mean MAE durations based on data from eight trials for each condition combination for each observer. The mean MAE durations from the four observers were then averaged across all conditions.

As shown in Appendix C, the MAE durations of observers AB and MvG were markedly greater across all conditions compared to those of MI and CV. However, despite this difference, it is important to note that, in general, a similar pattern of results was found after first- and second-order adaptation for all observers, suggesting that the difference in the MAE durations was quantitative and not qualitative. For this reason, MAE durations were average across observer and a single three-way ANOVA ((Eccentricity x Order Test Type (first- or second-order) x Motion Test Type (static or dynamic)) was conducted on the averaged data after both first- and second-order adaptation.

The ANOVA summary table of MAE durations after first-order adaptation is presented in Appendix D, Table 1. The mean MAE durations as a function of eccentricity and test type for first-order adaptation are shown in Figure 9a. As can be seen, MAE durations measured with different test types varied across eccentricity differentially. The non-significant Eccentricity x Order Test Type interaction found [$F(3,9)=0.236$, $p>.05$] showed that MAE durations measured with either first- or second-order patterns of the same motion type (static or dynamic) did not differ significantly at any eccentricity, suggesting that cross adaptation effects were present after first-order adaptation not at fixation, but also across eccentricity. As revealed by the significant Eccentricity x Motion Test Type interaction [$F(3,9)=17.144$, $p<.05$], the MAE durations measured with test patterns of different motion types (static or dynamic) varied differentially with eccentricity.

(a)

(b)
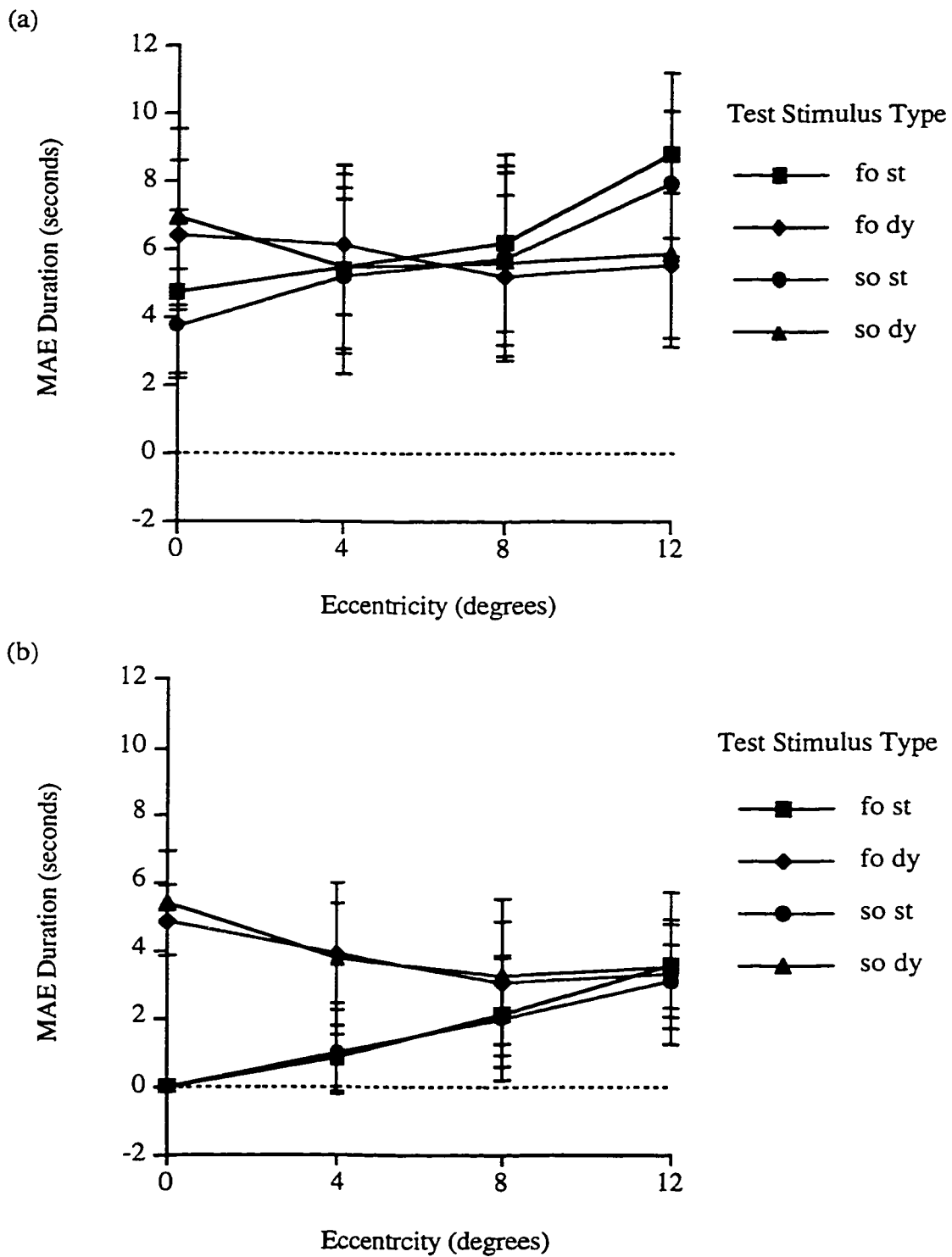
Figure 9. Mean MAE duration as a function of eccentricity and test stimulus
type after (a) first- and (b) second-order adaptation.

Simple effects (Appendix D, Table 2) showed that MAE durations measured with static test patterns (of any order type) increased significantly with eccentricity [$F(3,9)=31.535$, $p<.05$] whereas MAE durations measured with dynamic test patterns remained constant across eccentricity [$F(3,9)=2.577$, $p>.05$].

The ANOVA summary table of MAE durations after second-order adaptation is presented in Appendix D, Table 3. As was found after first-order adaptation, the Eccentricity x Order Test Type interaction was not significant [$F(3,9)=0.272$, $p>.01$], again suggesting cross adaptation effects across eccentricity after second-order adaptation. similar to the results after first-order adaptation, a significant Eccentricity x Motion Test Type interaction [$F(3,9)=32.484$, $p<.01$], was found after second-order adaptation. Simple effects (Appendix D, Table 4) revealed that MAE durations measured with static test patterns increased with eccentricity [$F(3,9)=9.364$, $p<.05$] whereas MAE durations measured with dynamic test patterns decreased with eccentricity [$F(3,9)=7.921$, $p<.05$].

Discussion

Although the overall results of all four observers were found to be qualitatively similar, inter-observer variability was evident. As mentioned in the Methods section of Experiment 1, although all four observers used in the adaptation study had previous psychophysical experience, only observers AB and MvG were familiar with MAE experimentation. One reason for the quantitative MAE duration difference between the experienced and inexperienced observers may have been the result of the paradoxical nature of the task, especially when static test patterns were used to measure MAE duration. Basically, observers were asked to respond when the illusory motion of a pattern ceased, a pattern which they knew was actually stationary. For the inexperienced observers, this paradox may have resulted in a more conservative response criterion, leading to the shorter MAE duration responses. The MAE data from a third inexperienced observer was omitted altogether because no MAE was reported after adaptation in most conditions, including those where the MAE was expected to be robust.

It must also be noted that the experimental design of Experiment 3 probably resulted in a task of elevated difficulty compared to most conventional adapt-test MAE studies. Eccentric stimulus presentation, testing with dynamic patterns in the periphery, used non-maximal adaptation contrasts and cross adaptation trials (adapt to first-order pattern and test with second-order pattern) may have all been factors which increased the difficulty of the task, especially for the inexperienced observers. However, despite the difference in overall MAE duration between the experienced and inexperienced observers, it is important to note that, in general, a similar pattern of results was found after first- and second-order adaptation for all observers, suggesting that the difference in the results was quantitative and not qualitative.

Cross-Adaptation Effects

As expected, cross-adaptation effects were present after both first- and second-order adaptation in the central visual field. For example, MAE durations measured with first-order static patterns were similar to those measured with second-order static patterns after both central first- and second-order adaptation, for all observers. The same was true for MAEs measured with dynamic tests in the central visual field. Results also showed that cross adaptation effects were not exclusive to central presentations but also present across eccentricity after adaptation to both motion types.

The presence of cross-adaptation effects across eccentricity implies that the technique used in Experiment 2 to approximately equate the visibility of first- and second-order motion patterns at each eccentricity was successful since it has been argued that cross-adaptation effects should result if first- and second-order patterns are matched for visibility and the presence of noise in the patterns (e.g., Ledgeway & Smith, 1994b). Although the visibility of the matched FO and the SO patterns used in the present experiment were just noticeably different, robust cross adaptation effects were found across eccentricity. The cross-adaptation effects found across eccentricity is a rather important finding since the alternate and more conventional method of equating the suprathreshold visibility of the two pattern types across eccentricity by applying a common multiple of direction-identification to both first- and second-order patterns may have not produced the same results. This may have been the case in this study in particular since it was found that the direction-identification thresholds between the first- and second-order patterns, to which the multiple would have been applied, increased with eccentricity at dissimilar rates (see Experiment 1).

As discussed by Ledgeway & Smith (1994b), cross-adaptation effects may not be appropriate criteria to discriminate between models proposing common, low-level (e.g., Grzywacz, 1992) or separate, parallel mechanisms (e.g., Wilson et al, 1992) of first- and

second-order motion processing since cross-adaptation effects can be interpreted as being the result of either a common, low-level mechanism (Turano, 1991) or separate, parallel first- and second-order mechanisms whose signals are integrated at a later processing stage (e.g., Wilson et al., 1992). If cross-adaptation effects do indeed reflect underlying processing of the two motion types, then the present results imply that whatever mechanism is responsible for central processing is also present for peripheral processing. However, the interpretation of the present and previous MAE cross-adaptation results (e.g., Ledgeway, 1994, Ledgeway & Smith, 1994) in order to address underlying motion mechanisms should be done with caution. Cross-adaptation results have also been found after adaptation to a plaid stimulus, whose visibility was matched to first-order and second-order dynamic and static test gratings, using the same procedure as the present study (von Grünau, Somekh & Bertone, 1998). Results from their study suggest that for one, cross-adaptation effects are not stimulus specific; for example, after adaptation to a moving plaid stimulus, the resulting MAEs measured with first- and second-order static grating patterns were similar. Therefore, cross-adaptation effects can be elicited even when adapt and test patterns are stimuli of different types. Secondly, if first- and second-order motion are detected at different levels along the visual pathway i.e., first-order motion at V1 and second-order motion at V2 or higher (MT) (e.g., Wilson et al., 1992), one would expect MAEs measured with first-order patterns to be larger than those measured with second-order patterns after adaptation to a transparently moving plaid since the component motions of the plaid are thought to be processed locally, by neurons in V1, and vise-versa, i.e., MAEs measured with a second-order test to be greater after coherent plaid motion. This, however, is not what was found. Although MAE duration was found to be independent of plaid coherence, no difference in MAE duration was found when measured with first- or second-order test patterns.

Based on the aforementioned reasons, the cross-adaptation effects found in the present study are interpreted strictly as the result of the first- and second-order patterns

being properly matched for visibility at each eccentricity, at least for the purpose of the present experiment. They will not, however, be interpreted on a theoretical basis since it is suggested that the cross-adaptation effects found in this study and others do not directly define nor discriminate between previously mentioned first- and second-order motion processing models.

Since no difference between first-and second-order test patterns of the same class (static or dynamic) was found after adaptation to both motion types, test types will be referred to as being either simply static or dynamic for the rest of the discussion.

Static MAEs After First- and Second-Order Adaptation Across Eccentricity

As mentioned in the Introduction, it has been suggested that the static MAE (sMAE) reflect the adaptation of low-level, or 'Fourier', motion mechanisms. It is therefore not surprising that static MAEs (sMAE) were elicited after central adaptation to the first-order patterns for all observers.

Results also showed that the duration of the sMAE increased significantly with eccentricity. This result has been explained by the fact that the spatial grain of visual processing is coarser in the periphery, where average receptive-field sizes are larger, increasing linearly with eccentricity (e.g., Hubel & Wiesel, 1974). For example, Wright and Johnston (1985) found that MAE strength, measured by the nulling with real motion, increased with eccentricity after adapting to non-scaled sinusoidal gratings. However, when the adapting stimulus size was spatially M-scaled (Rovamo & Virsu, 1979), the nulling velocity was found to be constant across the visual field. It was therefore concluded that the MAE mechanism is spatially scaled with eccentricity. Similarly, appropriately scaling the size and spatial frequency of the first-order patterns used in the

present study should result in constant sMAE durations across eccentricity after first-order motion adaptation.

Although the MAE properties after adaptation to first-order motion have been investigated in the periphery, albeit using a different method of magnitude estimation, the MAE properties of second-order motion have not. The presently well accepted result that a sMAE is not elicited after central adaptation to second-order motion is not only a defining property of second-order motion, but also a finding used to develop hypothetical models of first- and second-order motion processing. Essentially, it is theorized that second-order motion is processed at higher levels along the visual pathway after additional rectification and filtering stages before motion is detected. The result of adaptation of second-order motion is therefore measurable with dynamic test stimuli only, a test thought to access higher levels of motion processing. This suggests that first- and second-order motion are processed by distinct mechanisms along the visual pathways.

Results from the present study were therefore as expected after central (0 degrees) adaptation to second-order motion. For all observers, no MAE was found after second-order adaptation when tested with a static pattern. This result is consistent with the findings of previous second-order adaptation studies that have also shown that no sMAE is elicited after adaptation to a variety of second-order stimuli (e.g., Anstis, 1980; Derrington & Badcock, 1985; Ledgeway, 1994). As mentioned in the Introduction, this finding is consistent with motion models which propose that first- and second-order motion processing is carried out, at least initially, by separate low-level mechanisms which operate in parallel using similar principles of detection (e.g., Chubb & Sperling, 1988; Wilson et al., 1992).

The main purpose of the present study was to investigate second-order MAE properties in the periphery in order to address the question of whether or not the defining MAE properties of second-order motion were exclusive to central vision. The results of the static test condition after second-order adaptation in the periphery were unexpected. The

results showed that for all observers, adaptation to second-order motion produced a static MAE in the periphery, although no sMAE was produced after central adaptation (see Appendix C). At the most eccentric presentation (12 degrees), the size of the sMAE after second-order adaptation was comparable to, and in some cases, larger than the MAE measured with a dynamic test for all observers. For two observers (AB & MI), the sMAE was perceived only at higher eccentricities (i.e., 8 and 12 degree presentations) whereas sMAEs were perceived starting at 4 degrees for the other two observers (MvG & CV). For all observers, the sMAE was largest when presented at 12 degrees, the most eccentric presentation. Regardless of these inter-observer differences, the significant result found in the present experiment is that a clear static MAE was perceived after adaptation to second-order motion in the periphery.

This finding is inconsistent with previously mentioned models (e.g., Wilson et al., 1992; Nishida & Sato, 1994) of first- and second-order motion, which predict a sMAE after adaptation to first-order motion only. If the sMAE does indeed reflect the behaviour of low-level motion mechanisms (i.e., conventional motion detectors) along the visual pathway, then the present results indicate that in the periphery, static test patterns appears to be more sensitive to second-order motion adaptation than in central vision. It can be argued that if second-order motion is detected by a low-level mechanism in the periphery, then adaptation to second-order motion should result in sMAEs comparable to those produced after first-order motion adaptation. This result was found in the present experiment and can be interpreted as reflecting the existence of a common, low-level motion mechanisms in the periphery, which processes both first- and second-order motion effectively. Theoretical models proposing a common mechanism mediating both types of motion have been developed (Johnston et al., 1992; Grzywacz, 1992) but have not been empirically tested. These models have the advantage of parsimony over the models proposing separate first- and second-order motion mechanisms and therefore, may be better suited to account for

second-order motion processing in the periphery where there is less cortical representation relative to the fovea.

The interpretation that separate first- and second-order mechanisms mediate motion processing in central vision and that a common, low-level mechanism mediates peripheral motion processing is speculative. This possibility is based exclusively on the MAE results found in the present experiment, which on their own, do not directly address the question whether or not similar motion mechanisms are operating in central and peripheral visual fields. However, this possibility can be assessed using more direct techniques which test the integration of first- and second-order motion signals presented peripherally. These techniques will be described in detail in the General Discussion. Furthermore, to make theoretically sound comparisons between the predictive power of the different models in central and peripheral visual fields, it would be necessary to scale the size and spatial frequency of the first- and second-order patterns across eccentricity. However, the fact that non-scaled patterns were used in this study does not explain the sMAE following second-order adaptation in the periphery. In fact, it is not known whether scaled patterns will result in an attenuation or increase in the duration of the sMAE in the periphery (please see below).

Another factor that could potentially explain the production of a sMAE after second-order adaptation in the periphery may have to do with the changing characteristics of the static test pattern across eccentricity. The observers in this study were involved in making judgments on illusory motion of a stationary test pattern that paradoxically appeared to drift opposite the direction of the adapting pattern without changing its spatial location. A significant and possibly defining difference between static and dynamic test patterns may be their inherent difference in motion sensitivity. Static test patterns are defined by stationary spatial cues, which at some level, are processed and used as internal tags by the visual system, denoting an absence of movement at the retinal position occupied by the pattern. In order to perceive a sMAE, sufficiently strong motion signals coming from the temporary

imbalance of directionally selective mechanisms after adaptation must outweigh the stationary spatial cues of the stationary test pattern by a certain amount, or no MAE is perceived. The fact that the dynamic patterns do not contain such stationary cues may explain their increased sensitivity to second-order motion adaptation. The resulting motion signal may simply be too weak to override the spatial cues of a subsequently presented static test pattern in the center.

An important consideration might be that the stationary positional cues characterizing the static test may be more binding in central vision compared to the periphery, resulting in a 'static' pattern in the peripheral visual field which is not as 'static' as the one presented foveally. The precise position of patterns across the visual field is limited by the structure of the visual system. It is known that the spatial sampling grain of the visual cortex increases from the fovea to the periphery. As eccentricity increases, the size of the ganglion receptive field sizes increase while the density of cones and ganglion cells decreases with eccentricity. These changes are evidenced psychophysically by findings that $d\ max$, the spatial limit of apparent motion, increases with eccentricity (Kolers & von Grünau, 1977; Baker & Braddick, 1985). Since the receptive field sizes are larger in the periphery, apparent motion is perceived even when the scale of displacement is many times that of the fovea. These results, among others, reflect the possibility that the precision of a certain spatial position, or local sign (Hering, 1899), is limited by the spatial representation of the pattern in the periphery. If the position of these local signs become increasingly uncertain with eccentricity, then the position of static patterns presented in the periphery would not be as defined, or constrained to a spatial location compared to those presented centrally. If this were the case, and since the visibility of the second-order patterns were equated across eccentricity, motion signals produced by the central second-order adaptation might not have been enough to elicit a sMAE (not attaining the critical ratio) while a motion signal of the same strength in the periphery may have resulted in a

sMAE since the ratio needed to override the peripheral positional cues was lower, resulting in the sMAE.

An obvious way to test this hypothesis would be to scale the spatial frequency and size of the patterns across eccentricity. If a difference in 'staticness' does exist between centrally and peripherally presented test patterns, then scaling might attenuate the sMAE perceived in the periphery since position uncertainty of the test pattern will be decreased. However, if the peripheral, second-order motion signal is enhanced by the adaptation and test patterns, an increase in the sMAE may result.

Dynamic MAEs After First- and Second-Order Motion Across Eccentricity

Dynamic MAEs were expected after both first- and second-order motion adaptation when tested in the central visual field. MAEs were also measured in the periphery in order to compare their strength with those measured in the center. As expected, dynamic MAEs were elicited after both central and peripheral first- and second-order adaptation for all observers. Results show that in general, dMAEs were constant across eccentricity after first-order adaptation for all observers. However, inter-observer differences were found for dMAE durations after second-order adaptation. Although, constant MAE durations were found across eccentricity for the two practiced observers (AB & MvG), the strength of the dMAE decreased with eccentricity for the other two. This was especially true for observer MI, whose dMAE was about half of the sMAE at 12 degrees after second-order adaptation.

Since the contrast of the test and adapting patterns were matched across eccentricity (as evidenced by the cross-adaptation effects), the decreasing dMAE durations with eccentricity for the inexperienced observers may have been the result of the increased difficulty of the task, especially in the periphery. Since a sMAE was found after second-

order adaptation, one would have expected a dMAE of at least the same duration since it is presumably measured with a more sensitive test.

Overall, the dMAE results were not unexpected as both first- and second-order motion have been shown to produce MAEs if tested with dynamic test patterns. Scaling the size and spatial frequency of the patterns may decrease the difficulty of the task since larger patterns presented in the periphery will allow observers to maintain a constant response criterion across eccentric presentations.

GENERAL DISCUSSION AND CONCLUSIONS

It has been nearly a decade since the terms 'first-order' and 'second-order' motion (Cavanagh & Mather, 1989) were introduced to visual motion research. Since then, a number of psychophysical studies have been undertaken in order to evaluate the dichotomy and the models describing their underlying mechanisms. Although models proposing a single motion-detection mechanism (Johnston et al., 1992; Grzywacz, 1992) have been shown to be theoretically compatible with some of the results from second-order studies (e.g., Turano, 1991), the majority of the amassed findings from second-order motion studies supports models that postulate the existence of separate, low-level motion mechanisms for first- and second-order motion. Probably the most substantial psychophysical evidence reflecting the existence of separate mechanisms is the now well-accepted fact that a sMAE is not elicited after adaptation to second-order motion although a robust sMAE is perceived after first-order motion adaptation. This second-order property has been interpreted as evidence that the two motion-types being processed, at least initially, by separate mechanisms before being integrated at a higher level along the visual pathway.

However, these models are based exclusively on central MAE properties of first- and second-order motion. In an attempt to better understand how mechanisms analyze first- and second-order motion, it may be helpful to explore how their properties vary as a function of position in the visual field. The main purpose of the present study was therefore exploratory in nature; to define the MAE properties of second-order motion in both central and peripheral fields of vision in order to address whether or not these properties and the underlying mechanisms are exclusive to central vision. This was also done in comparison to first-order motion.

In order to equate the visibility of the first- and second order adaptation and test patterns across eccentricity for the main experiment in this study, two preliminary

experiments (Experiments 1 & 2) were conducted which in themselves provided additional defining properties of the two motion types across eccentricity. In the first experiment, direction-identification thresholds were measured for the two motion-types across eccentricity. Results showed that the motion sensitivities of the two motion types declined with eccentricity at dissimilar rates as the sensitivity of second-order motion declined significantly faster with eccentricity compared to that of first-order motion. These finding are interpreted as being the result of the two motion types being detected by separate mechanisms mediating the detection of their respective motion in central and peripheral fields of vision.

The results from these experiments also have implications for the methodologies of future studies. They demonstrate the need to equate the visibility of first- and second-order patterns across eccentricity. The results of Experiment 2 show that the relationship between approximately matched first- and second-order suprathreshold visibility changes with eccentricity. Using the subjectively matched visibilities in the adaptation experiment, cross-adaptation effects were found after both first- and second-order adaptation for both static and dynamic test conditions. These results suggested that the visibility of the first- and second-order patterns were properly matched at each eccentricity. Using the more conventional method of applying a common multiple of direction-identification threshold to both stimulus classes in order to equate their visibility may not be the method of choice. By equating the visibility with a common multiple at each eccentricity, it is assumed that the direction-identification thresholds, from which the multiple is derived, increase at similar rates for both motion types. The results of Experiment 1 showed that this wasn't the case, at least for the patterns used in this study. This assumption was avoided entirely in the present experiment by matching the suprathreshold contrasts of first- and second-order patterns individually at each eccentricity using a method of direct comparison.

Using the first- and second-order patterns matched for visibility in Experiment 2, the MAE properties of first- and second-order motion were assessed in both central and

peripheral fields of vision using static and dynamic tests in Experiment 3. Although the central MAE properties of first- and second-order motion have been defined and are generally well accepted, their peripheral MAEs, especially those of second-order motion, have not been systematically assessed. As mentioned in the discussion of Experiment 3, the novel and unexpected finding of the adaptation study was the production of a sMAE after adaptation to second-order motion in the periphery. Firstly, it can be concluded that the currently accepted defining MAE properties of second-order motion are exclusive to central vision. Secondly, the finding that a sMAE is perceived after second-order adaptation in the periphery has important theoretical implications on currently accepted motion models, which, in part, are based on the findings of MAE studies. The present results were interpreted as evidence for different motion mechanisms mediating second-order motion processing in central and peripheral vision. Specifically, since both first- and second-order motion result in a sMAE after peripheral adaptation, the possibility exists that a common, low-level mechanism is mediating both motion types in the periphery, the adaptation of which is reflected by the sMAE. This hypothesis, however, is based entirely on the MAE data from Experiment 3 and should be investigated further using more direct methods.

The findings from several psychophysical studies suggest that distinct mechanisms exist for the detection of first- and second-order motion, with each mechanism being sensitive to one motion type (e.g., Harris & Smith, 1992; Ledgeway, 1994; Nishida et al., 1994). In particular, motion integration studies using periodic stimuli have provided compelling evidence favouring the distinct mechanism hypothesis (Mather & West, 1993; Ledgeway & Smith, 1994a). For example, Ledgeway & Smith (1994) used a multiframe motion sequence composed of alternating first- and second-order frames which were successively phase-shifted 90 degrees. The parameters of the motion sequences were set so that an unambiguous percept of apparent motion in a certain direction would result if the first- and second-order motion signals would interact. However, separate analysis of the

two types of frames would lead to ambiguous motion. Results showed that observers were not able to integrate the first- and second-order frames. These results were interpreted as direct evidence favouring models which suggest separate motion detecting mechanisms for each motion type.

In order to better evaluate the possibility that a common motion mechanism is operating in the periphery, the same motion sequence test can be presented peripherally. If observers are able to integrate first- and second-order frames, it can then be suggested that the two types of motion are detected by a common, low-level mechanism. Such a finding would extend and support the MAE results of Experiment 3, which suggested that different types of motion-detecting mechanisms are operating in the central and peripheral visual fields; separate mechanisms for the two motion types in the center and a common mechanism for both types in the periphery. Consequently, this would demonstrate the exclusivity of current models based on MAE properties for central vision.

An important methodological issue to be considered for future investigations of second-order motion properties in the periphery is spatial scaling. For performing a variety of visual tasks, the peripheral visual system seems to be as efficient as the central system (e.g., Virsu & Rovamo, 1979) if the stimuli are scaled since an approximately constant number of cells are involved in the processing of the stimuli at each eccentricity. Although there is no apriori reason for expecting qualitatively different results with scaled patterns than the ones that were found in the present study, i.e., the absence of a static MAE in the periphery, it can be argued that the different cortical representation of patterns may affect the second-order MAE properties across eccentricity. It has been shown, however, that the reduction of motion sensitivity of certain second-order patterns is dependent on eccentricity and not on pattern size (Zanker, 1997). Nonetheless, the scaling of adaptation and test patterns would provide more conclusive evidence regarding definitions and possible distinctions of second-order motion mechanisms operating in central and peripheral visual fields.

In conclusion, the results from the present study demonstrated that well-accepted second-order MAE properties defining second-order motion processing in central vision differ from those in the periphery. These results are interpreted as evidence for the existence of distinct mechanisms underlying second-order motion processing in the central and peripheral fields of vision.

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APPENDIX A

<u>ANOVA Summary Tables for Mean Threshold Modulation Depths as a Function of Eccentricity for First- and Second-Order Motions Separately and Relatively (After Standardization)</u>

Table 1

ANOVA Summary Tables for Mean Threshold Modulation Depths (% Modulation) as a Function of Eccentricity for First-Order Motion

Source	df	SS	MS	$\underline{F}$
Within Subjects				
Eccentricity	3	.364	.123	10.272**
Error	9	.108	.012	

*$\underline{p}$ < .05.   **$\underline{p}$ < .01.

Table 2

ANOVA Summary Table for Mean Threshold Modulation Depths (% Modulation) as a Function of Eccentricity for Second-Order Motion

Source	df	SS	MS	F
Within Subjects				
Eccentricity	3	2157.924	719.308	14.922**
Error	9	433.839	48.204	

*p < .05.   **p < .01.

Table 3

ANOVA Summary Table for Mean Relative Sensitivity (dB) as a Function of Eccentricity for Both Motion Types

Source	df	SS	MS	$\underline{F}$
Within Subjects				
Motion Type	1	166.695	166.695	16.997**
Error	3	29.4232	9.423	
Eccentricity	3	326.668	108.889	42.981***
Error	9	22.801	2.533	
Motion Type x Eccentricity	3	64.740	21.580	6.303**
Error	9	30.812	3.424	

*$\underline{p}$ < .05.   **p < .025   **$\underline{p}$ < .01.

APPENDIX B

<u>ANOVA Summary Table for Mean Matched (FO*) and Multiple of Common Threshold</u>

<u>(FO Common) First-Order Suprathreshold Modulation Depths as a Function of Eccentricity</u>

Table 1

ANOVA Summary Table for Mean Matched (FO*) and Common Multiple of Threshold (FO Common) First-Order Suprathreshold Modulation Depths as a Function of Eccentricity

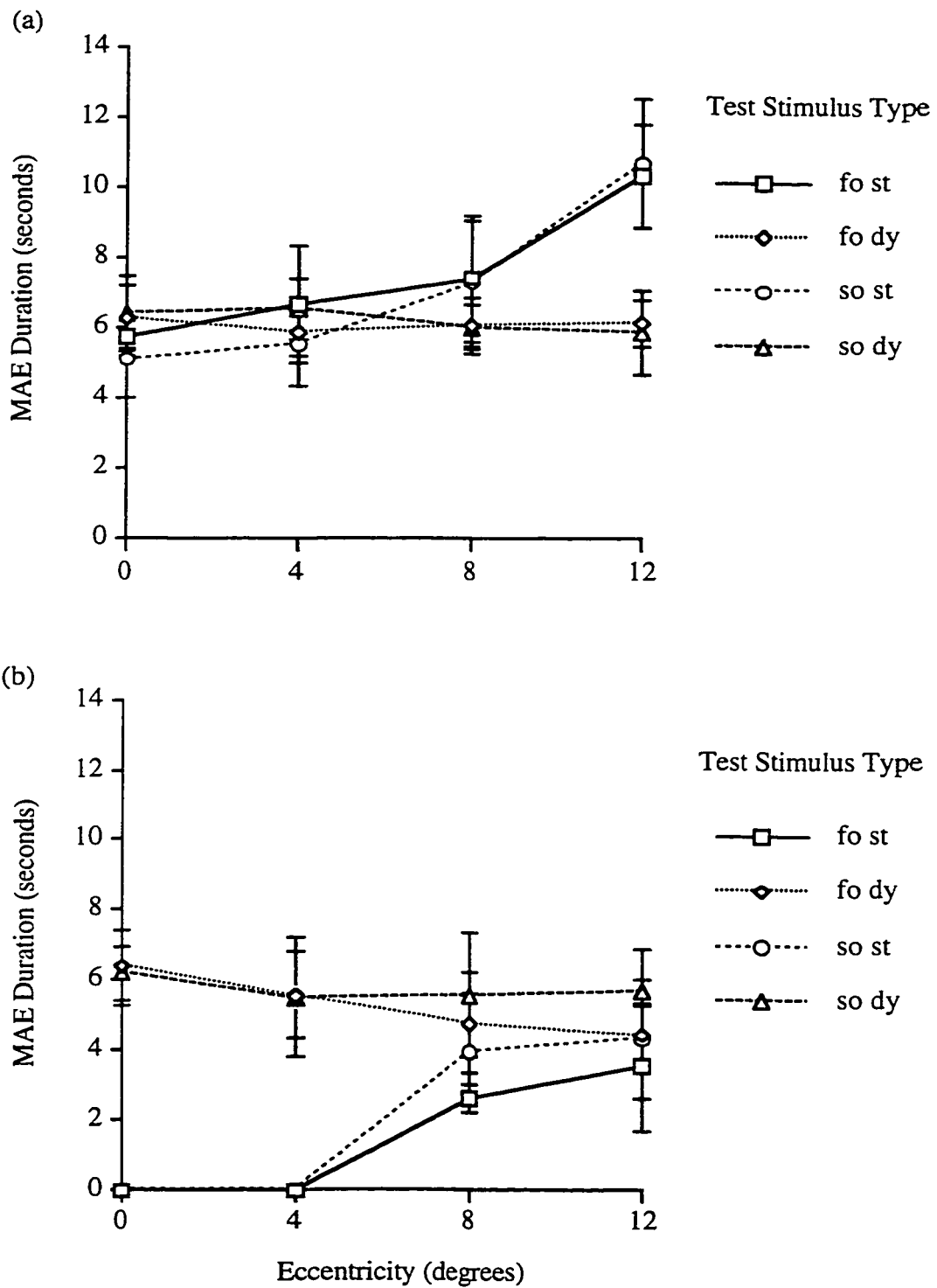| Source	df	SS	MS	F
Within Subjects				
Motion Type	1	4298.962	4298.962	23.847**
Error	3	540.807	180.269	
Eccentricity	3	514.763	171.588	8.170**
Error	9	1481.009	164.557	
Motion Type x Eccentricity	3	431.388	143.796	6.277*
Error	9	206.173	22.908	

*p < .05.   **p < .01.

APPENDIX C

MAE Durations as a Function of Eccentricity and Test Stimulus Type

After First- and Second-Order Adaptation for Each Observer

(a)

(b)

MAE duration as a function of eccentricity and test stimulus type after (a) first- and (b) second-order adpatation for observer AB.
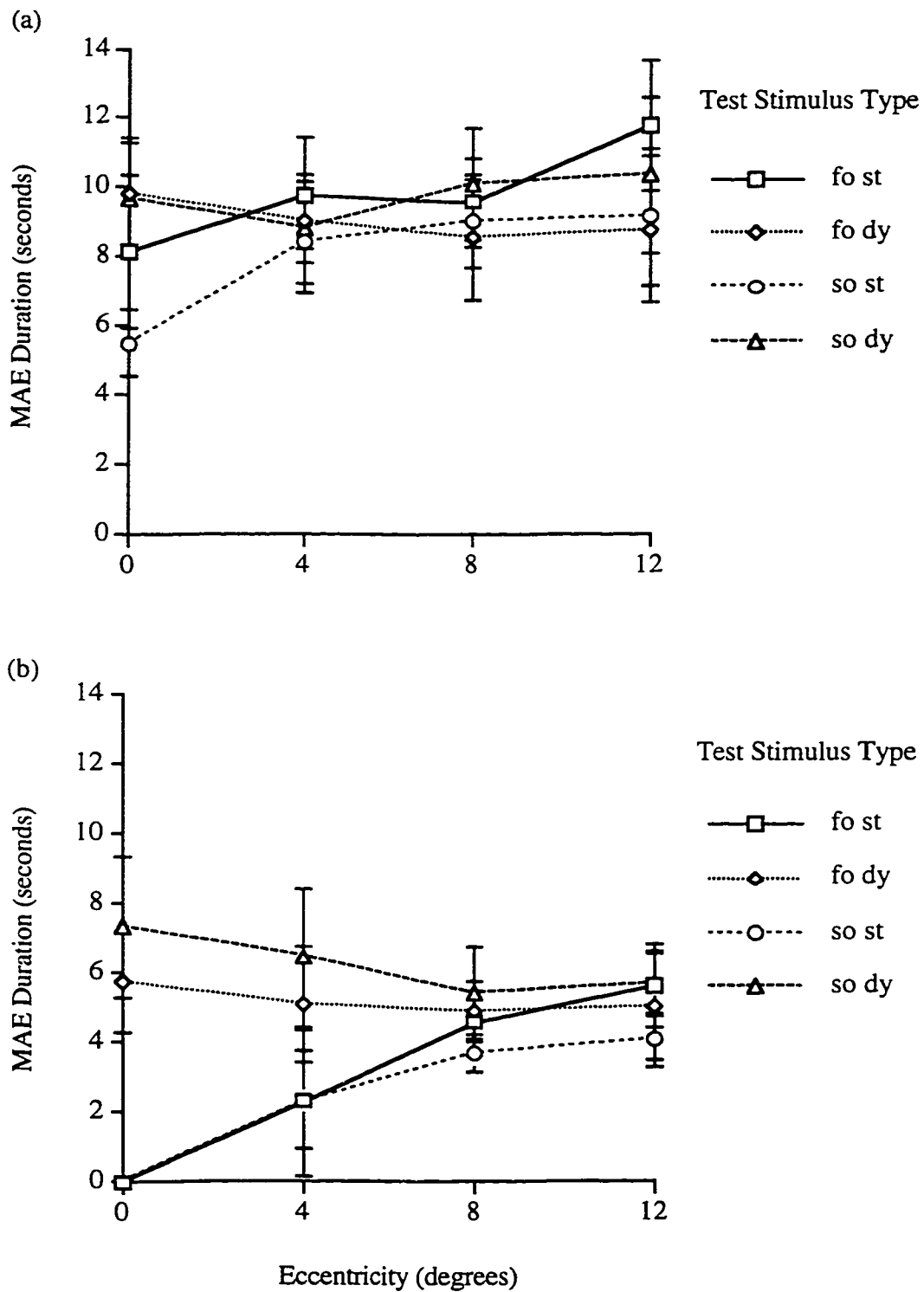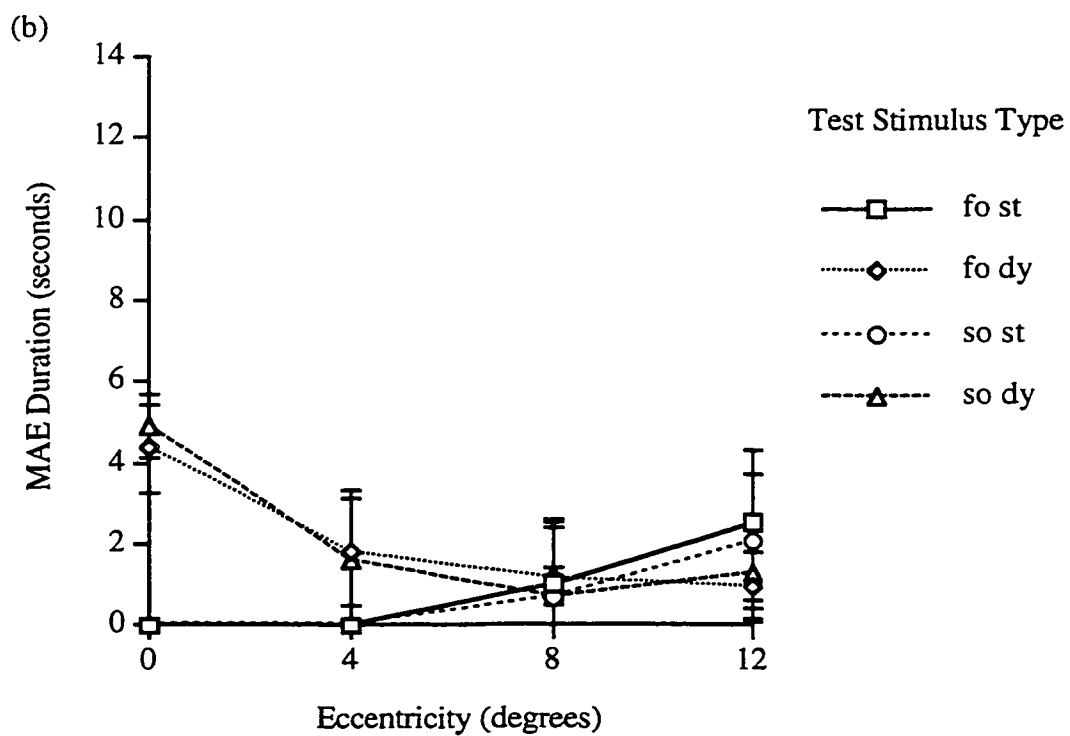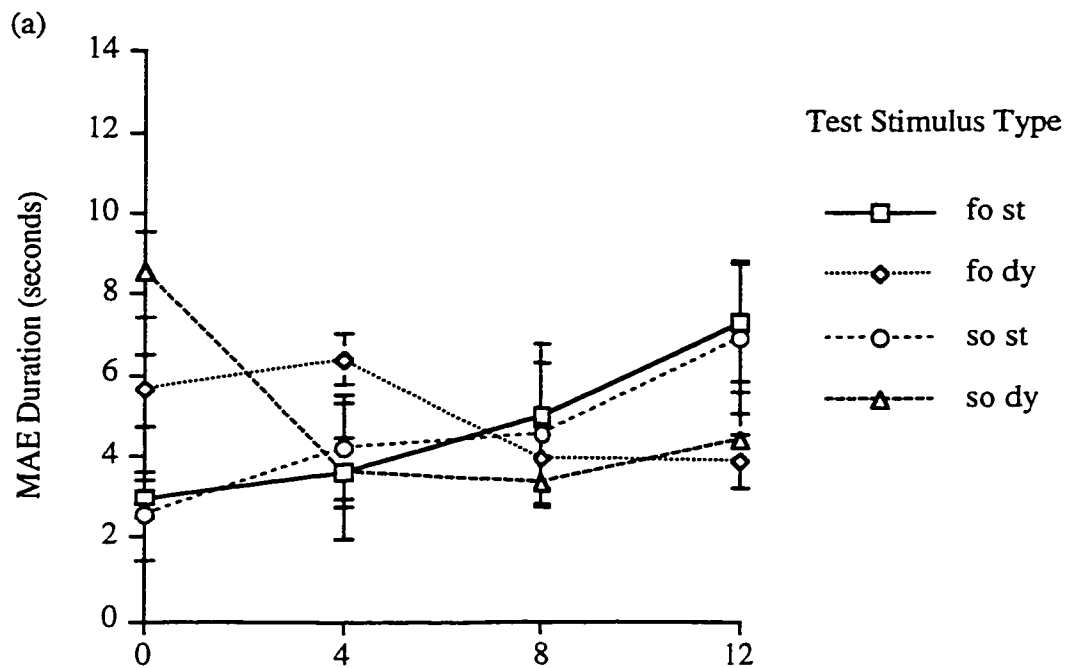
(a)

(b)

MAE duration as a function of eccentricity and test stimulus type after

(a) first- and (b) second-order adpatation for observer MvG.

MAE duration as a function of eccentricity and test stimulus type after
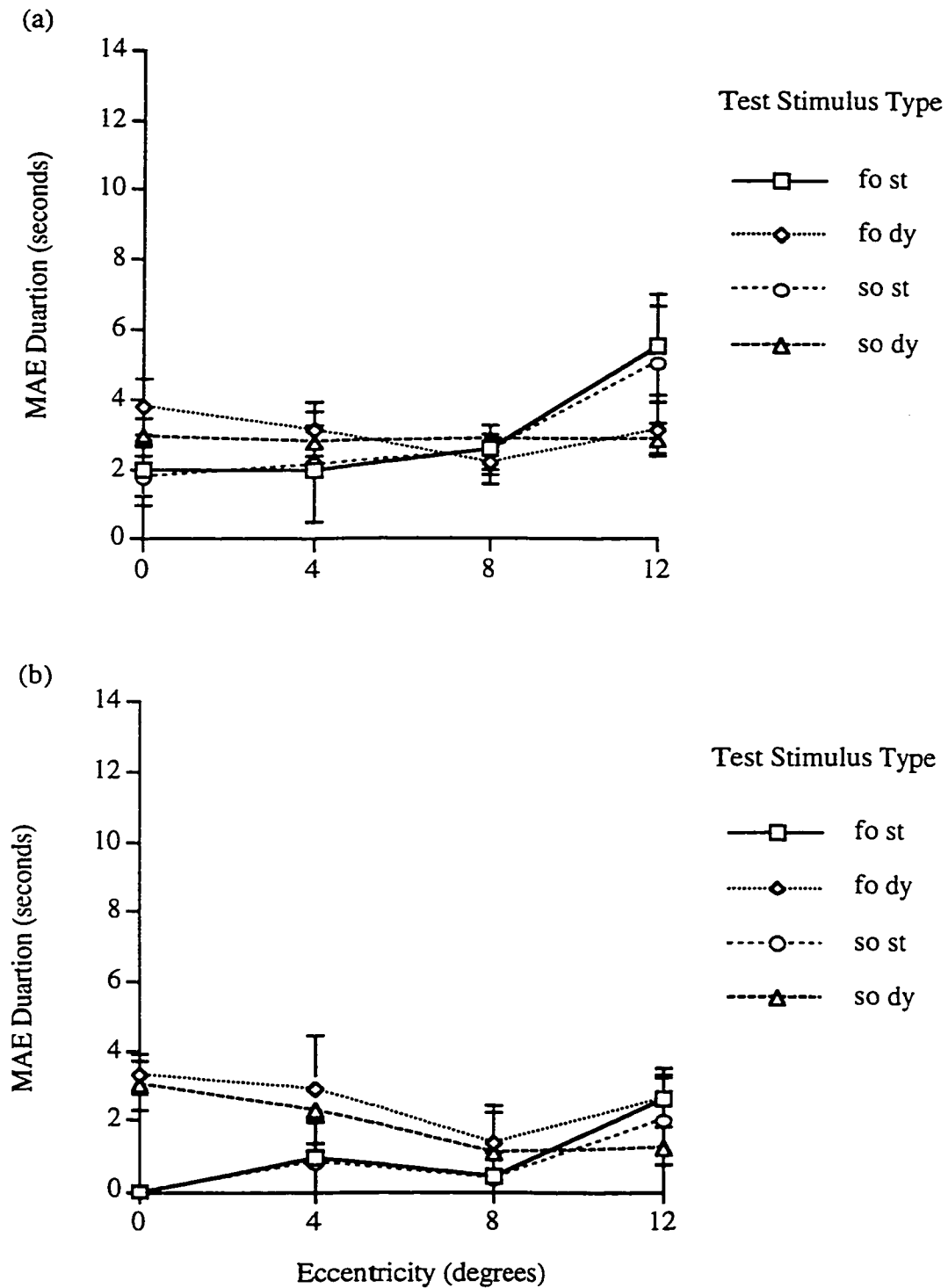(a) first- and (b) second-order adpatation for observer MI.

(a)

(b)

MAE duration as a function of eccentricity and test stimulus type after

(a) first- and (b) second-order adpatation for observer CV.

APPENDIX D

ANOVA Summary Table and Subsequent Analyses on MAE Duration as a

Function of Eccentricity, Order Test Type and Motion Test Type after Both

First- and Second-Order Adaptation

Table 1

ANOVA Summary Table of MAE Duration as a Function of Eccentricity, Order Test Type (OTT) and Motion Test Type (MTT) After First-Order Adaptation

Source	df	SS	MS	F
Within Subjects				
Eccentricity	3	26.066	8.689	13.587**
Error	9	5.755	0.639	
Order Test Type (OTT)	1	0.908	0.908	4.673
Error	3	0.583	0.194	
Eccentricity x OTT	3	0.366	0.122	0.236
Error	9	4.650	0.517	
Motion Test Type (MTT)	1	0.101	0.101	0.043
Error	3	7.015	2.338	
Eccentricity x MTT	3	53.665	17.888	17.144**
Error	9	9.390	1.043	
OTT x MTT	1	2.412	2.412	1.674
Error	3	4.321	1.440	
Eccentricity x OTT x MTT	3	2.080	0.693	0.848
Error	9	7.360	0.818	

*$p < .05$.   **$p < .01$.

Table 2

Simple Effects of Eccentricity on MAE Duration for Each Motion Test Type After First-Order Adaptation Across Eccentricity

Source	df	SS	MS	F
Motion Test Type				
Static Test Type (fo st & so st)	3	72.660	24.220	31.535**
Error	9	6.912	0.768	
Dynamic Test Type (fo dy & so dy)	3	7.071	2.357	2.577
Error	9	8.235	0.915	

*$p < .05$.   **$p < .01$.

Table 3

ANOVA Summary Table of MAE Duration as a Function of Eccentricity, Order Test Type (OTT) and Motion Test Type (MTT) After Second-Order Adaptation

Source	df	SS	MS	F
Within Subjects				
Eccentricity	3	9.202	3.067	1.543
Error	9	17.890	1.988	
Order Test Type (OTT)	1	0.017	0.017	0.020
Error	3	2.447	0.816	
Eccentricity x OTT	3	0.316	0.105	0.272
Error	9	3.492	0.388	
Motion Test Type (MTT)	1	83.396	83.396	15.603*
Error	3	16.034	5.345	
Eccentricity x MTT	3	60.684	20.228	32.484**
Error	9	5.604	0.623	
OTT x MTT	1	0.340	0.340	0.532
Error	3	1.919	0.640	
Eccentricity x OTT x MTT	3	0.535	0.178	2.499
Error	9	0.643	0.071	

*$p < .05$.   **$p < .01$.

Table 4

Simple Effects of Eccentricity on MAE Duration for Each Motion Test Type After Second-Order Adaptation Across Eccentricity

Source	df	SS	MS	F
Motion Test Type				
Static Test Type (fo st & so st)	3	50.940	16.980	9.364**
Error	9	16.317	1.813	
Dynamic Test Type (fo dy & so dy)	3	18.948	6.316	7.921**
Error	9	7.173	0.797	

*p < .05.   **p < .01.