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# Eye movements provide the extra-retinal signal required for the perception of depth from motion parallax

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## Abstract

It has been unclear whether the perception of depth from motion parallax is an entirely visual process or whether it requires extra-retinal information such as head movements, vestibular activation, or eye movements. Using a motion aftereffect and static test stimulus technique to eliminate visual cues to depth, this psychophysical study demonstrates that the visual system employs a slow eye movement signal, optokinetic response (OKR) in particular, for the unambiguous perception of depth from motion parallax. A vestibular signal, or vestibularly driven eye movement signal is insufficient for unambiguous depth from motion parallax. Removal of the OKR eye movement signal gives rise to ambiguous perceived depth in motion parallax conditions. Neurophysiological studies suggest a possible neural mechanism in medial temporal and medial superior temporal cortical neurons that are selective to depth, motion, and direction of eye movement.

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## 1. Introduction

The visual perception of depth is crucial to an observer moving through a cluttered environment (Frey & Owen, 1999). Helmholtz observed that the visual system uses motion parallax to generate a vivid, unambiguous depth percept as if the observer were looking with two eyes using binocular stereopsis (von Helmholtz, 1909/1962). Indeed, similar to the spatial geometry of stereopsis, the temporal geometry of motion parallax has an orderly relationship to the relative distances of the objects in the scene (Braunstein & Andersen, 1984; Gibson, 1950; Rogers, 1993). These orderly geometric relationships make both binocular stereopsis (Howard & Rogers, 1995; Ohzawa, DeAngelis, & Freeman, 1990) and motion parallax (Gibson, Gibson, Smith, & Flock, 1959; Rogers & Graham, 1979) useful cues to relative depth. Unfortunately, we know little about the neural systems involved in the perception of depth from motion parallax.

Motion parallax is the change in relative position of stationary objects at different distances from the vantage point of a moving observer. That is, as an observer translates, objects at various positions in the landscape create a changing pattern on the observer's retina. Objects more distant than the point of gaze move on the retina in the same direction as the translating observer, while nearer objects move in the opposite direction on the retina (Gibson, 1950). The requisite observer translations that produce this retinal motion may be either small active lateral head movements, or more sustained passive translations such as those produced by riding in a vehicle and viewing out the side window, a stimulus condition originally coined as motion perspective (Gibson, 1950). Both active and passive conditions generate the same retinal motion and very similar eye movements. Consider that when an observer moves, actively or passively, the eyes move in the opposite direction to maintain fixation on the scene (Miles & Busettini, 1992). Due to these compensatory eye movements, the point of fixation remains stationary on the observer's retina while objects at various distances move relative to one another on the observer's retina. The visual system does not usually interpret these retinal motions as actual movements of the objects in the environment (Ono &

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Steinbach, 1990). Instead, the visual system uses motion parallax to determine each object's depth relative to the fixation point and cancels any perception of object movement (Leigh & Zee, 1999).

One crucial problem for understanding how the visual system recovers depth from motion is to explain why the resulting depth percepts are unambiguous in situations such as motion parallax, but ambiguous or depth reversing in other conditions with similar retinal movement. For instance, in the classic kinetic depth effect (KDE) a stationary observer views a flat shadow of a rotating wire (Wallach & O'Connell, 1953) or Lissajous figure (Smith, 1976) and perceives a vivid, but ambiguous, depth percept fluctuating between two opposite depth interpretations. To understand this, investigators have examined the contributions of both visual and extra-retinal processes in the perception of depth from motion (Rogers & Rogers, 1992). It has been well established that visual cues including perspective information (Braunstein & Andersen, 1981; Braunstein & Tittle, 1988) and binocular disparity (Nawrot & Blake, 1991; Rogers & Graham, 1982; Rogers & Graham, 1984) may disambiguate the perception of depth from motion. However, Ono and Ujike's (1994) use of the motion aftereffect (MAE) and a static stimulus to produce motion parallax shows that extra-retinal information is essential. In their study, all visual cues to depth, including retinal motion, visual perspective, and binocular stereopsis, were eliminated. Perceived depth in a static, and otherwise depthless, test stimulus was determined by the direction of observer head movement. Their result cannot be explained by visual factors alone.

A vestibular signal regarding self movement has been the most obvious source of extra-retinal information for motion parallax (Gibson et al., 1959; Rogers & Rogers, 1992; Steinbach, Ono, & Wolf, 1991). However, since the earliest studies (Rogers & Graham, 1979) we have known that stimulus display movement viewed by a stationary observer is just as effective as observer head movements in generating unambiguous motion parallax. Therefore, observer movement, and its concomitant vestibular signal, are not necessary for unambiguous depth from motion parallax. Even more, the unambiguous depth percept is opposite for head movements and display movements in the same direction (Rogers & Graham, 1979). Considering that these two conditions with opposite depth percepts elicit slow eye movements in opposite directions, the extra-retinal information used in determining depth sign in the perception of depth from motion parallax might come from the slow eye movement system.

One important role of the slow eye movement system is to maintain fixation as an observer moves. To accomplish this, both visual and vestibular systems work together to generate a compensatory slow eye movement, a vestibular ocular response (VOR), 180 deg out

of phase with the head movement (Leigh & Zee, 1999; Paige & Tomko, 1991). The conditions for motion parallax specifically engage the translational VOR which operates independently of the more well known rotational VOR (RVOR) system (Miles & Busetini, 1992). During abrupt observer translation the translational vestibular ocular response (TVOR) originates with the vestibular otolith organs. This TVOR system is characterized by short latency (Bronstein & Gresty, 1988) and the gain of this system varies with viewing distance (Bronstein & Gresty, 1988; Busetini, Miles, & Schwarz, 1991; Oas, Baloh, Demer, & Honrubia, 1992; Schwarz, Busetini, & Miles, 1989; Schwarz & Miles, 1991). With viewing distances less than one or two meters, large eye movements are required and the TVOR gain is less than one, which is too small to keep the fovea centered on the point of fixation. Therefore, to maintain perfect fixation, the optokinetic reflex (OKR) is triggered by the retinal slip generated by the eyes losing fixation due to inadequate TVOR. The OKR combines with TVOR to achieve gain equal to one (perfect fixation). Serving this function, it appears that both the TVOR and OKR mechanisms feed into a single eye movement generator (Busettini et al., 1991; Schwarz et al., 1989) and both are subserved by the same neural mechanism, the corticoponto-cerebellar system, as opposed to the pretectum/accessory optic system for rotational VOR system (Miles & Busetini, 1992). Even more specifically, it appears that the OKR has two independent components with the early or direct component, called OKNe, serving as a visual augmentation for the TVOR. The second component, the delayed or indirect component, OKNd, is associated with RVOR (Busettini et al., 1991; Cohen, Matsuo, & Raphan, 1997). Moreover, the OKNe component of OKR shares many functional and physiological similarities with visual pursuit mechanisms (see Miles & Busetini, 1992 for a review). For the purpose of this manuscript, the visually driven component of the compensatory eye movement will be referred to as OKR, although more research is needed to clarify the similarities and differences between OKR, OKNe, and pursuit eye movements as they relate to the perception of depth from motion parallax.

It is important to note that this same slow eye movement system is used during passive moving conditions that give rise to conditions that Gibson (1950) described as motion perspective. With sustained observer translation and large viewing distances, for instance the conditions present during driving, TVOR is more-or-less inactive and OKR alone serves to maintain fixation on a point in the scene viewed through the window. Therefore, OKR eye movements are present during both active and passive observer translation and could serve as an extra-retinal signal for motion parallax. The current psychophysical study addresses this possibility and investigates the role of head movements,

TVOR and OKR eye movements, in the unambiguous perception of depth from motion parallax.

## 2. General method

Four different experiments used an identical adaptation/test procedure based on Ono and Ujike's (1994) parallaxic MAE technique. In all experiments the perception of parallaxic depth was created with a MAE rather than with actual retinal movement. This MAE paradigm allowed the same static test stimulus, four rows of small vertical bars, to be projected onto the same retinal location in every trial of every experiment. This use of a static test stimulus precluded any depth information being generated by stimulus motion perspective, stimulus differential transformation, stimulus relative motion, or stimulus velocity gradient. While this static test stimulus does convey a very small (4 arc min) linear perspective transformation created by observer head translation, this transformation is the same for all four rows and therefore cannot serve to differentiate the relative depth of the rows within the stimulus. In all cases, the only difference between the four rows in the test stimulus is the MAE created in the observer's brain, not any type of retinal information. In all four experiments the test stimulus was identical: four rows of small vertical bars with a small fixation cross at the center. In all experiments the proximal test stimulus remained stationary on the observer's retina (within the limits of the compensatory eye movement system to maintain perfect fixation). Therefore, systematic differences in the perceived depth of this stimulus are due solely to the extra-retinal information available to the observer.

Observers adapted for 30 s to the MAE stimulus described in Fig. 1. Observers fixated a stationary cross at the center of the MAE adaptation stimulus. All viewing was monocular. The stimulus area was  $6.6 \text{ deg}^2$ . Each horizontal row consisted of 10 vertical bars, each  $1.5 \text{ deg}$  in height and  $0.33 \text{ deg}$  in width. Bars moved at  $2.2 \text{ deg/s}$ . Alternate rows moved in opposite directions. The particular directions of MAE adaptation movement in each trial were counter-balanced throughout the experiment as were the directions of head, eye, or stimulus movement as required in particular experiment. Following the MAE adaptation, observers viewed a static test stimulus with the phase of the bars aligned in the four rows. As noted by Ono and Ujike (1994), observers experienced a normal MAE when viewing the stationary test stimulus. When observers made head translations along the interaural axis, in combination with the MAE, observers perceived the test stimulus as stationary with regard to lateral movement but also alternating rows of bars were perceived as standing out and recessed back in depth relative to the fixation point (Fig. 1C). The sign of perceived depth reversed with a reversal in the direction

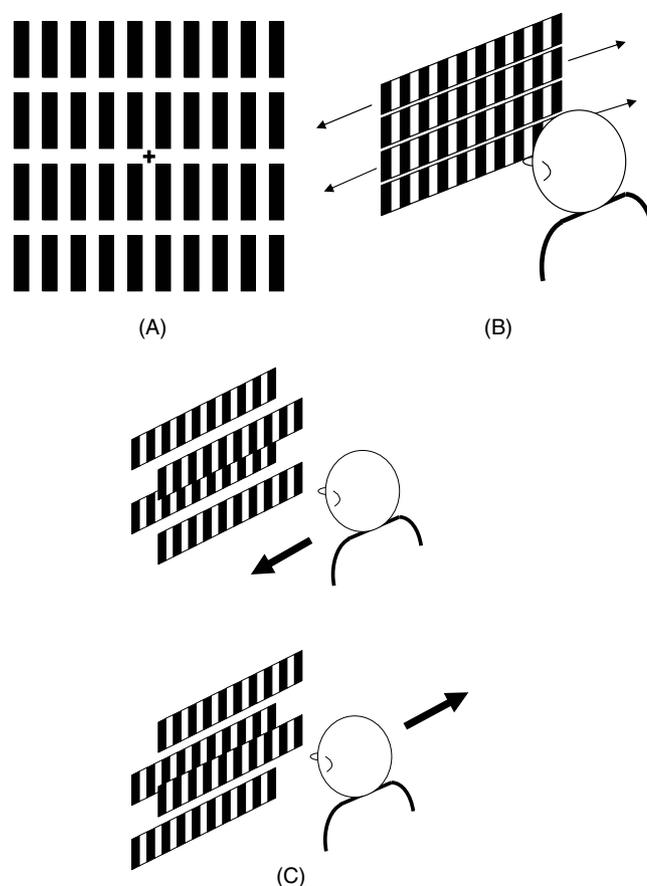


Fig. 1. Schematic of the stimulus used in these experiments. The visual stimulus comprises four rows of small vertical bars (A). Observers adapt to movement of the rows, each row translating leftward or rightward in the direction opposite the row next to it. Upon viewing a static version of this stimulus, observers perceive a MAE as the rows appear to move in the direction opposite the adaptation motion (B). When this illusory MAE movement is coupled with head translations along the interaural axis, rows with MAE in the direction opposite the direction of head movement appear to stand out in depth (C). Perceived depth switches when the head movement is made in the opposite direction.

of observer head movement. The perceived depth disappeared when observers stopped making head movements and the bars resumed their illusory movement due to the MAE.

The observer's task in every trial was to indicate which row, above or below the fixation point, appeared nearer in depth. For instance, "above" is the correct response for the top panel in Fig. 1C while "below" is the correct response for the lower panel. Each observer completed three separate sessions totaling 48 trials in each experiment. All viewing was monocular and observers wore an eye patch over the unused eye. Three observers (author and two naive observers) participated in the first three experiments and five observers (original plus two additional naive observers) participated in the last experiment. In the data analysis,  $p$  values were derived from binomial approximation, while  $d'$  values

derived from a look-up table (Macmillian & Creelman, 1991).

### 3. General apparatus

Psychophysical stimuli were presented on a monochrome monitor viewed from a distance of 57 cm. Observer head position was restricted to translation along the interaural axis through use of a bite bar affixed to a slide moving along a pair of rails on linear bearings. A high viscosity silicone dental putty (Exaflex, GC America; Chicago, IL) was used to make an impression on the metal bite bar which was rigidly connected to the slide. The bite bar firmly prevented observer head movement in the other five dimensions. Lateral translation of the slide required an almost insignificant force averaging 0.96 N (SD = 0.25 N). Position of the head movement slide was monitored with a linear potentiometer (ETI Systems; Carlsbad, CA). Head position along the 20 cm slide movement was determined to the nearest 0.1 mm with stop-to-stop device linearity of  $r^2 = 0.999$ . Due to the bite bar device constraining movement to the interaural axis and preventing any tilt or roll of the observer's head, observers typically moved their heads only within the central 12 cm of the device. Observers were instructed to make smooth cyclical head movements with a cycle taking about 2 s (0.5 Hz). Although viewing time was unrestricted in the test phase of each trial, observers typically performed the task quickly with only a single head movement required to make the depth judgement about the stimulus.

Eye position was determined by head mounted infrared monitory (Skalar; Delft, Netherlands). Eye monitory was only used during observer familiarization and training to ensure that observers could simultaneously fixate, move their heads, and perform the psychophysical portions of the task. The number of psychophysical trials required of each observer, and the need for frequent recalibration, precluded the use of eye monitory during data collection. Head movement and eye movement devices were connected to the computer through a 12 bit ADC (National Instruments; Austin, TX).

## 4. Experiment 1

### 4.1. Procedure

In the first experiment the test stimulus remained stationary on the display while the observer's head translated left and right. Observer eye movements compensated to maintain fixation on the test stimulus during head movements (Fig. 2). To implement this technique as a 2AFC paradigm, and allow the observer multiple viewings if necessary, a particular direction of

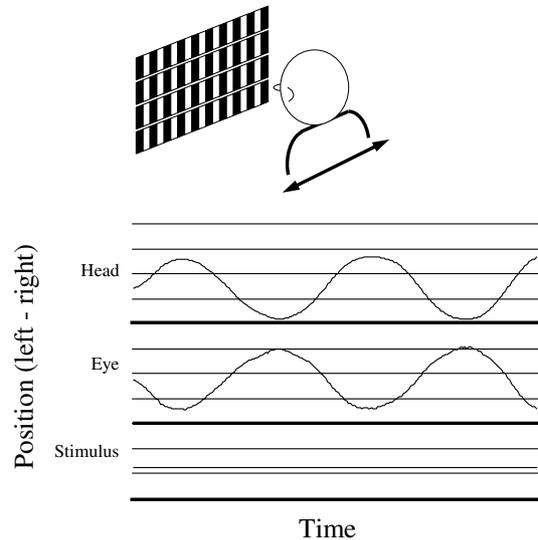


Fig. 2. Recordings of the head, eye, and stimulus movements from one observer while performing a practice trial of the task. The horizontal axes denote time. The vertical axes denote horizontal position in raw values (the changes in each tracing is the important feature). In experiment one, the stimulus remained stationary, the head moved back and forth, and the eyes moved in the opposite direction in phase with the head movements.

observer movement was selected as the test direction for each trial. When the observer moved in the specified direction for that trial, the static test stimulus was displayed and the observer reported which row of bars, either above or below the fixation point, appeared nearer in depth. When the observer moved in the opposite direction, the test stimulus was blanked and only the fixation point was displayed. This prevented the perceptual reversal seen with head movements in the opposite direction and made a simple 2AFC paradigm possible.

### 4.2. Results

On 95% of the trials ( $p < 0.001$ ,  $d' = 2.2$ ) perceived depth in the stationary test stimulus was determined by the direction of observer head and eye movement. Stimulus rows generating a MAE in the direction opposite observer head movement were perceived as near while rows with MAE in the opposite direction were perceived as farther away than fixation. That is, the identical pattern of MAE yielded opposite depth percepts with head movements in opposite directions, confirming the observations made by Ono and Ujike (1994). Because the retinal stimulus was stationary and MAE is independent of observer movement, this result demonstrates that the perception of depth from motion parallax relies on an extra-retinal signal arising from the observer's head movement. That is, regardless of the direction of MAE, the direction of observer movement and the perceived depth order, the retinal test stimulus

was the same. Of course, in this experiment head movement, TVOR eye movements and OKR eye movements covaried perfectly. The subsequent experiments attempt to separate and isolate the role of each in the perception of depth from motion parallax.

### 5. Experiment 2

#### 5.1. Procedure

Head movements were removed in the second experiment thereby eliminating both vestibular activation due to abrupt observer translation and TVOR eye movements. Following adaptation, the observer used pursuit or OKR eye movements to maintain fixation on a test stimulus as it moved across the display (Fig. 3). The entire test stimulus was shown only as it moved in one direction, and only the fixation cross returned back across the display in the opposite direction to guide the observer’s slow eye movements. To prevent all head movements and vestibular activation, and concomitantly all vestibularly driven eye movements, the observer’s head was fixed via a bite bar and did not translate.

#### 5.2. Results

Similar to the result from the first experiment, on 99% of the trials ( $p < 0.001$ ,  $d' = 3.3$ ) MAE movement in the same direction as the eye movements was perceived nearer than fixation. Of course, these are the stimulus conditions for motion perspective (Gibson, 1950): relative stimulus movement (created by MAE here) and

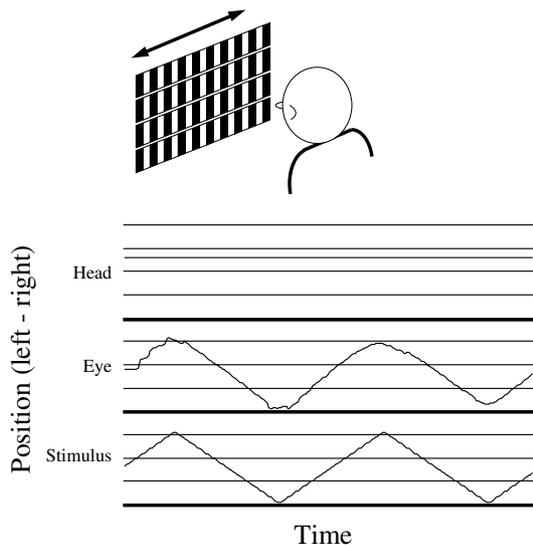


Fig. 3. In experiment 2, head movements were eliminated. Observers used eye movements to maintain fixation as the test stimulus moved back and forth across the screen.

OKR eye movements, with no head movements and no vestibular activation. This result confirms, with a different technique, the report of Rogers and Graham (1979) that stimulus movement without observer movement is sufficient for the unambiguous perception of depth from motion parallax. This result indicates that the necessary extra-retinal signal comes from the OKR eye movement, not a vestibular signal, or a vestibularly driven eye movement signal such as TVOR.

### 6. Experiment 3

#### 6.1. Procedure

In the third experiment eye movements were eliminated although the observer’s head still moved back and forth. In this experiment the test stimulus was yoked to, and moved along with, the observer’s head movements (Fig. 4). To maintain fixation on the test stimulus the observer’s eye must remain stationary within the observer’s head. However, this does not mean that internal eye movement signals were eliminated. Instead, this test stimulus condition elicited OKR eye movements in the direction of the head movement in order to “cancel” or suppress the TVOR eye movements in the direction opposite the head movement (Tomlinson & Robinson, 1981). The net result of this cancellation is that the eyes remained stationary in the head. Again, the test stimulus was shown only during head movements in one of the

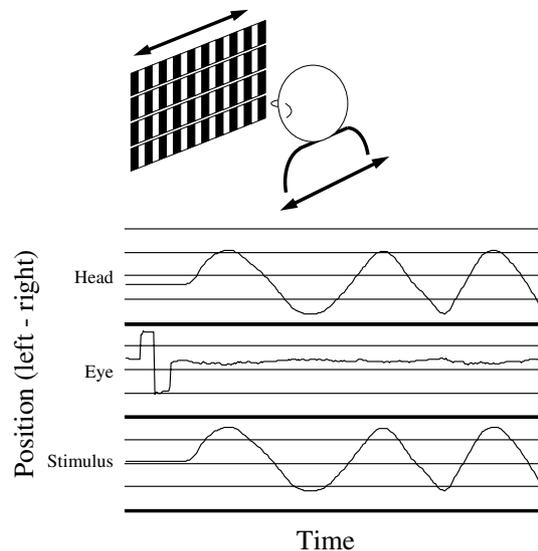


Fig. 4. In experiment 3, the stimulus moved back and forth as if fixed to the observer’s head. The eye remained stationary within the orbit. The small square wave at the beginning of the eye movement tracing was the observer making a saccade to the right and to the left before head movements were initiated thereby showing how steady the eyes remained in the orbit when the head movements were initiated.

two directions with only the fixation cross visible during movements in the opposite direction.

This experiment uncouples the relationships between head movement/TVOR (which are inseparably linked) and OKR. This makes it possible to determine which of these extra-retinal signals is required in the perception of depth from motion parallax. In typical motion parallax conditions, head movements and compensatory eye movements are in opposite directions and TVOR and OKR are usually in the same direction. In the current experiment this contingency is reversed: head and OKR movements are in the same direction, while TVOR and OKR are in opposite directions. If MAE in the same direction as eye and head movements is perceived nearer than fixation, this would mean that the OKR signal is used in the perception of depth from motion parallax. However, if MAE in the opposite direction is perceived near, this would mean that the head movement and TVOR signals are used in the perception of depth from motion parallax.

## 6.2. Results

MAE movement in the same direction as the eye and head movements was perceived near on 91% of the trials ( $p < 0.001$ ,  $d' = 1.9$ ). If head movement or TVOR provide the extra-retinal signal, MAE movement in the opposite direction would have been perceived near, the relationship found with the typical stimulus conditions of motion parallax. Therefore, this experiment suggests that OKR eye movement is the source of the extra-retinal signal in the perception of depth from motion parallax.

## 7. Experiment 4

### 7.1. Procedure

To test the hypothesis that OKR eye movements are the source of the extra-retinal signal in the perception of depth from motion parallax, OKR eye movements were removed in a final experiment. If OKR provides the signal for the unambiguous perception of depth from motion parallax, the system should break down when this signal is eliminated. Typically, TVOR is isolated by testing in total darkness (Baloh, Yue, & Demer, 1995; Paige, Telford, Seidmen, & Barnes, 1998; Paige & Tomko, 1991). However, this was unfeasible in this experiment due to the visual nature of the psychophysical task: observers must see the test stimulus to perform their task. Therefore, OKR was prevented by appropriate movement of the test stimulus linked to observer head movement. Consider that eye movements in lighted, near viewing conditions are a product of both TVOR and OKR and typically have a gain (eye position

divided by head position) very close to one. For instance, in preparation for this experiment pilot testing at 57 cm viewing distance yielded a mean light gain = 1.0 (SD = 0.04). However, eye movements in dark conditions are products of TVOR alone as there is no visual stimulus and therefore no retinal slip signal to drive OKR. Typically the gain of TVOR at near viewing distances is less than one (Paige & Tomko, 1991) and pilot testing in preparation for this experiment yielded a mean dark gain = 0.80 (SD = 0.05). Since both research and models suggest a linear combination of VOR and OKR (Crane, Virre, & Demer, 1997; Paige, 1983; Schwarz et al., 1989; Schweigart & Mergner, 1995; Schweigart, Mergner, & Barnes, 1999), subtraction of dark gain (TVOR alone) from light gain (TVOR+OKR) provides the OKR component. In the pilot testing mentioned above, on average, 20% of the compensatory eye movement signal was due to OKR.

To determine the OKR gain, and therefore the magnitude of stimulus movement, compensatory eye movements were measured in light and dark conditions immediately before each session for each observer (Fig. 5). In light conditions observers fixated a small spot on the display and made lateral head movements while both head and eye movements were monitored. In dark conditions observers were instructed to fixate the same spot, but the display was both extinguished and occluded as the observer began a head movement. The observer was to imagine that the spot was still visible and to keep their fixation on it while moving his or her head back and forth, even though the room was completely, and immeasurably, dark (0.000 lux; J17 Photometer, J1811 Illuminance Head; Tektronix; Beaverton, OR). Light gain and dark gain were determined from the average of the first four half cycles. Subtraction of the dark gain (TVOR alone) from the light gain (TVOR+OKR) gives the OKR gain for that observer for that particular session. For instance, if the light gain

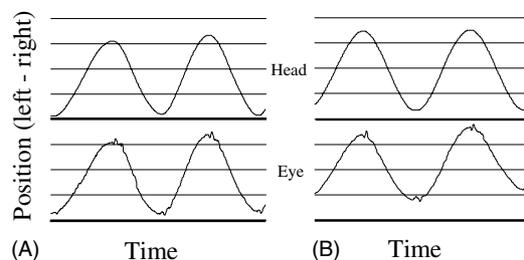


Fig. 5. Shown are typical head and eye movements used to determine light and dark gain values. The sign of the eye movement recording was reversed so that the two tracings could be shown in phase making it easier to compare the eye movement gain in the two conditions. (A) In the example shown, the light gain (TVOR and OKR) is 1.05 and (B) dark gain (TVOR alone) is 0.88. The amplitude of the eye movement decreased slightly in the dark condition due to the loss of the OKR component in complete darkness.

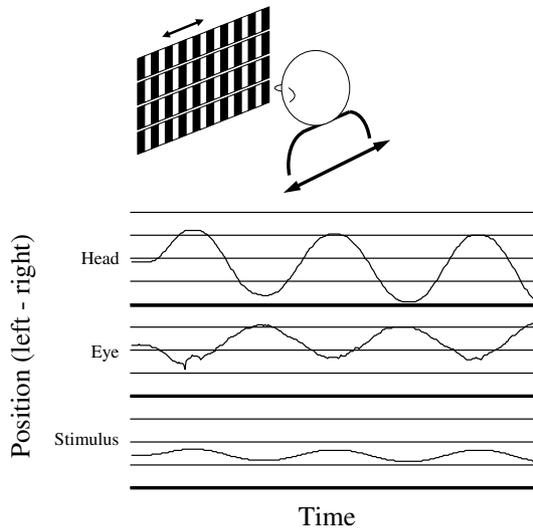


Fig. 6. In experiment four, the stimulus moved a small proportion of the observer's head movement in an attempt to position the test stimulus where the TVOR system would position the eyes, thereby preventing OKR eye movements.

value were 1.0, and the dark gain value were 0.80, the OKR gain would be 0.20.

The OKR gain value was determined for each session for each observer and was used to adjust test stimulus movement so that the test stimulus would be where TVOR positioned the observer's eye (Fig. 6). For instance, if OKR gain were 0.20, the test stimulus would move on the screen in the direction of the observer's head movement with 20% of the magnitude of the observer's head movement. In this way the test stimulus would be positioned exactly where the TVOR guided the observer's eye position. So positioned, the retinal slip that drove the OKR was avoided. That is, by moving the test stimulus proportional to the OKR gain, the test stimulus would always be where the under-compensating TVOR positioned fixation. With this stimulus movement preventing OKR, the perception of depth from motion parallax should be disrupted if OKR eye movement signals are indeed used by the motion parallax mechanism.

## 7.2. Results

MAE movement in the same direction as the TVOR eye movement was perceived nearer than fixation on only 49% of the trials ( $p=0.60$ ,  $d'=-0.04$ ). Unlike the results of the previous experiments, there was no consistent relationship between MAE motion, perceived depth, and direction of head movement or TVOR eye movement. Instead, observers were 98% ( $p < 0.001$ ,  $d'=2.9$ ) consistent in reporting a particular direction of MAE movement as being nearer, regardless of the direction of head or eye movement. That is, four observers

reported that rightward motion was nearer than fixation and one observer reported that leftward motion was nearer, regardless of head movement direction. This means that the stimulus conditions were ambiguous, and observers were expressing a bias in the perception of depth from motion. Indeed, subsequent testing showed that observers reported the same motion/depth biases when viewing ambiguous rotating KDE figures. Following each session observers viewed orthographic projections of rotating spheres and cubes and were asked to report the direction that the front, or near surface, of the figure appeared to move (Nawrot & Blake, 1989). Observers were instructed to maintain fixation on a small cross at the center of the figure. In 86% of trials ( $p < 0.001$ ,  $d'=1.53$ ) observers reported that the direction of KDE motion perceived in near depth was the same as the direction of motion that they had perceived in near depth in Experiment 4. This suggests that the same underlying perceptual bias is seen with KDE and by removing the OKR eye movements in motion parallax stimulus conditions.

This experiment shows that the perception of depth from motion parallax is rendered ambiguous by elimination of OKR. Therefore, it appears that OKR eye movements provide the extra retinal signal for the perception of unambiguous depth motion parallax. Moreover, it is likely that the depth ambiguity resulting from the removal of OKR and the depth ambiguity observed with KDE stimuli are linked. Perhaps perceived depth from motion parallax and from KDE are the product of the same "depth-from-motion" mechanism operating with and without eye movement inputs. In motion parallax, the removal of the OKR eye movement signal creates a "null" eye movement condition and the mechanism receives insufficient information to determine an unambiguous depth order. The mechanism still generates depth from motion, but without OKR it has no information to disambiguate depth order. The result is depth from motion, with the same perceptual biases emerging as seen when viewing a KDE figure with stationary eyes.

## 8. Discussion

When presented with otherwise ambiguous visual information, the unambiguous perception of depth from motion parallax relies on an extra-retinal signal in the form of OKR eye movements. It appears that depth order is computed through a neural implementation of a simple heuristic: retinal motion in the same direction as OKR is nearer than fixation while retinal motion in the direction opposite OKR is farther away than fixation. Additionally, Ono and Ujike (1994) have shown that the MAE will readily serve the role of retinal motion in this heuristic. While this MAE result carries the important

implication that depth from motion occurs in a neural processing stage subsequent to MAE, for this study its importance was methodological: in all four experiments the proximal retinal test stimulus was the same identical static figure fixed upon the same retinal location. The reversal in perceived depth seen in these experiments was due solely to different directions of eye movements. Explanations for motion parallax that rely solely on motion perspective (e.g., Braunstein and Tittle, 1986) have difficulty explaining the pattern of results created with this MAE motion parallax paradigm.

A neural mechanism subserving motion parallax must show motion selectivity, depth selectivity, and now eye movement selectivity. Primate studies have found neurons in medial temporal (MT) and medial superior temporal (MST) cortical areas that show precisely these selective response properties. Neurons in area MT are both depth and motion selective (Bradley, Qian, & Andersen, 1995; Maunsell & Van Essen, 1983), and changes in neuronal activity coincide with subjective changes in perceived motion and depth configuration when viewing an ambiguous rotating KDE stimulus (Bradley, Chang, & Andersen, 1998). Similarly, MST neurons display a combination of depth and motion selectivity relative to the plane of fixation (Roy, Komatsu, & Wurtz, 1992; Roy & Wurtz, 1990). In particular, the direction of motion selectivity in some MST neurons reverses as the stimulus depth, relative to the plane of fixation reverses. Other neurons in MST discharge during visual pursuit, with this response beginning after pursuit onset suggesting a perceptual, not visuo-motor, function (Komatsu & Wurtz, 1988a; Komatsu & Wurtz, 1988b; Newsome, Wurtz, & Komatsu, 1988). The preferred direction of these cells is opposite the direction of the pursuit movement, and this preferred direction of motion can reverse with a change in size or speed of the visual motion. Other MST cells are selective to the portrayal of multiple depth planes (Upadhyay, Page, & Duffy, 2000). The characteristics of these neurons are very similar to the characteristics required to account for motion parallax: self-movement with opposing directions of motion on opposite sides of the fixation plane with a response that changes with a change in the direction of eye movements.

One aspect yet to be resolved is the lack of perceived stimulus movement accompanying the perception of depth from motion parallax. In contrast, the ambiguous perception of depth from KDE is accompanied by perceived stimulus motion. In the current experiments, and Ono and Ujike's (1994) original demonstration, the MAE movement is converted into perceived depth. No illusory MAE movement is perceived during observer eye movements. This suppression of perceived motion, along with the OKR signal required for motion parallax, suggests a corollary discharge or efferent copy sys-

tem (Teuber, 1960). Although there is some controversy about whether OKR contributes to the efferent copy (Post & Leibowitz, 1985), and about the form the efferent copy signal (Wertheim, 1994), it is clear that some such signal is used to null perceived motion in motion parallax displays such as the one used here. A reasonable explanation is that an efferent copy of the OKR, or more specifically the pursuit-like OKNe (Miles & Busetini, 1992), might serve double duty both to cancel the perception of visual motion and to disambiguate the perception of depth from motion parallax. Indeed, it appears MST neurons are involved in such "post-comparator" processing as required by the stimulus conditions for motion parallax (Newsome et al., 1988). Perhaps it is at this stage where relative motion is converted into perceived depth through comparison with the OKR eye movement signal. In this way the neural mechanisms provide a parsimonious accounting for phenomenological aspects of the perception of depth from motion parallax.

The current study demonstrates that eye movement direction determines the perception of near/far depth order in a motion parallax stimulus. This is similar to the role of binocular disparity sign in determining near/far depth order for binocular stereopsis. In both cases, a reversal of the stimulus conditions results in a reversal in the sign of perceived depth. Moreover, there is emerging evidence that eye movement velocity influences magnitude of perceived depth from motion, similar to the way disparity magnitude is used to scale magnitude of perceived depth in binocular stereopsis. Freeman and Fowler (2000) found that eye movements influence the perceived slant of a surface defined by a velocity gradient. Following up their work on the mis-perception of a motion stimulus during slow eye movements (Freeman, 1999; Freeman & Banks, 1998), Freeman and Fowler (2000) found that perceived slant of a surface defined by motion perspective decreased as eye pursuit velocity increased. This result might be considered a form of depth-from-motion scaling based on eye movement velocity. Consider that low eye movement velocity is needed to maintain fixation on objects translating in the distance and increasing eye movement velocity is required as the translating object is seen with shorter viewing distances. Similarly, Nawrot (2000) demonstrated that perceived depth in a motion parallax stimulus scales inversely with the gain of the OKR eye movement component. Consider the case of a translating observer: as described earlier, TVOR gain decreases with shorter viewing distances and therefore larger OKR gain is required to maintain fixation. In both Freeman and Fowler (2000) and Nawrot (2000) the magnitude of the slow eye movement had an inverse relationship to the magnitude of perceived depth. This is further evidence that slow eye movements have a role in the perception of depth from motion.

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