ELSEVIER

Available online at www.sciencedirect.com

ScienceDirect

Vision Research 46 (2006) 4709–4725

Vision Research

www.elsevier.com/locate/visres

The pursuit theory of motion parallax

Mark Nawrot *, Lindsey Joyce

Center for Visual Neuroscience, Department of Psychology, North Dakota State University, Fargo, North Dakota, USA

Received 1 March 2006; received in revised form 7 July 2006

Abstract

Although motion parallax is closely associated with observer head movement, the underlying neural mechanism appears to rely on a pursuit-like eye movement signal to disambiguate perceived depth sign from the ambiguous retinal motion information [Naji, J. J., & Freeman, T. C. A. (2004). Perceiving depth order during pursuit eye movement. *Vision Research, 44*, 3025–3034; Nawrot, M. (2003). Eye movements provide the extra-retinal signal required for the perception of depth from motion parallax. *Vision Research, 43*, 1553–1562]. Here, we outline the evidence for a pursuit signal in motion parallax and propose a simple neural network model for how the pursuit theory of motion parallax might function within the visual system. The first experiment demonstrates the crucial role that an extra-retinal pursuit signal plays in the unambiguous perception of depth from motion parallax. The second experiment demonstrates that identical head movements can generate opposite depth percepts, and even ambiguous percepts, when the pursuit signal is altered. The pursuit theory of motion parallax provides a parsimonious explanation for all of these observations.

Keywords: Motion parallax; Pursuit; Depth; Eye movement

1. Introduction

Knowledge of the depth, position, and movement of objects and obstacles is crucial for successful locomotion. Depth perception is of such great importance that the human visual system relies on redundant sources of visual depth cues. These include static pictorial cues such as linear perspective, interposition, and relative size. However, two cues, binocular stereopsis and motion parallax, have the greatest importance due to the unambiguous relative depth metric they provide. While the neural mechanisms serving binocular stereopsis have been an active topic of study for decades, the basic neural processes involved in motion parallax have received little study and are still poorly understood.

Motion parallax is created by translation of the observer's optical viewpoint, but not by rotation. During a translation of the observer's optical viewpoint, the relative position of objects at different positions in the scene shift relative to each other. However, during a pure rotation (around the nodal point of the eye) the relative position of these objects does not change. Moreover, during this crucial translation the observer's head, the visual system maintains fixation on a particular point in the scene by moving the eyes in the direction opposite the translation. This pattern of head translation and ocular compensation generates a retinal stimulus from which an observer can recover relative depth information. Similar to stereopsis, where binocular retinal disparity sign (crossed vs. uncrossed) signals opposite depths relative to fixation, with motion parallax, objects moving in opposite directions on the retina are perceived at opposite depths relative to the stationary point of fixation. Again, similar to stereopsis, in which the magnitude of retinal disparity is proportional to the object's depth from the fixation point, with motion parallax, each object's retinal speed is proportional to that object's depth from the fixation point. However, unlike disparity, this retinal stimulus for motion parallax is inherently ambiguous with regard to depth sign because there is no visual information to determine which direction of retinal motion is nearer than fixation and which direction of retinal motion

---

* Corresponding author. Fax: +1 701 231 8426.
E-mail address: mark.nawrot@ndsu.edu (M. Nawrot).

0042-6989/$ - see front matter © 2006 Elsevier Ltd. All rights reserved.
doi:10.1016/j.visres.2006.07.006

is farther away than fixation (Farber & McConkie, 1979). This depth sign ambiguity is most evident with the kinetic depth effect (KDE) where a rotating figure may spontaneously reverse perceived depth interpretations making the figure appear to rotate in the opposite direction. Alternatively, the ambiguous KDE figure may simultaneously appear to rotate in opposite directions for two different observers.

For motion parallax, recent work (Naji & Freeman, 2004; Nawrot, 2003a, 2003b) suggests that the visual system uses an eye movement signal to disambiguate the depth sign of the motion parallax information. This manuscript will first outline how this might be accomplished in the visual system and then present a set of experiments demonstrating that this pursuit theory of motion parallax accounts for perceived depth in a variety of different viewing conditions.

Despite our poor understanding of the neural mechanisms serving motion parallax, its practical importance was actually recognized centuries ago. For instance, Wheatstone (1839), who developed the stereoscope and demonstrated the importance of retinal disparity and thus provided the theoretical foundation to understand the relation between retinal disparity and binocular stereopsis, also recognized that when binocular stereopsis failed, another "more ambiguous" depth cue relying on "motion of the head" could still provide cues to depth (Wheatstone,1838, cited in Wade, 1998, p. 292). Even earlier, French artist and mathematician, Phillipe de La Hire (1694, cited in Wade, 1998, p. 357) noted, "The parallax of objects is what we use most to recognize distance…" Perhaps recognizing the importance of eye movements, de La Hire continues "… when the eye moves to the right the object that thus appears to move away from the other to the right is further away". Helmholtz (1909/1962) is also well known for noting that the perception of depth from motion parallax is often as vivid as that generated by binocular stereopsis (see Ono & Wade, 2005 for a historical perspective).

Gibson (1950) rekindled interest in motion parallax by noting the importance of visual information created by an observer moving through an environment. Gibson even suggested different names for slightly different conditions of observer movement. If the observer is undergoing sustained translation, as in a vehicle, this creates *motion perspective*, while *motion parallax* "implies that the animal in question must move its head from side to side to obtain the cue for depth (Gibson, 1950, p. 128 footnote)." Both conditions create compensatory eye movements, although the particular mechanisms differ somewhat. The theory outlined here provides account of both conditions with the same visual processing mechanism thereby suggesting that both are products of the same underlying neural mechanisms.

In contrast to Gibson, some doubted the utility of motion parallax as a depth cue (Epstein & Park, 1964; Gogel & Tietz, 1977) and considered motion parallax to be dynamic variation of the static pictorial depth cue known as linear perspective. However, a pivotal demonstration by Rogers and Graham (1979) convincingly established that motion parallax is an independent cue for relative depth perception (motion parallax does not provide absolute distance information). Rogers and Graham used an electronically generated random-dot display wherein individual dot movement was linked to translation of the observer's head. The motion within this display simulated the transformation generated by an actual three-dimensional surface viewed with lateral head movement. When viewing this random-dot display upon the flat surface of the monitor, observers perceived a static corrugated surface with vivid and unambiguous depth. Moreover, Rogers and Graham (1979) demonstrated that an unambiguous motion parallax depth percept could be generated for a stationary observer by linking stimulus dot translation to the lateral translation of the entire display monitor. This is a third viewing condition (stationary observer) capable of creating unambiguous depth from motion parallax, along with conditions wherein observers actively make head translations or passively translate in which as in a vehicle. A parsimonious theory of depth from motion parallax must account for all three of these stimulus conditions in the unambiguous depth from motion parallax is perceived.

1.1. Eye movements in motion parallax

An important question for understanding the neural mechanisms for motion parallax is whether an extra-retinal signal is required for the unambiguous depth from motion parallax. And, if so, what is the source of the extra-retinal signal? While some are equivocal (Rogers & Rogers, 1992), others suggest that visual motion decomposition is used to disambiguate the relative depth of the visual motion signal (Braunstein & Andersen, 1981; Braunstein & Tittle, 1988; Gibson, Gibson, Smith, & Flock, 1959; Hershberger & Starzec, 1974; Koenderink, 1986). However, a purely visual model, without an extra-retinal signal, has difficulty explaining the demonstration provided by Ono and Ujike (1994) who used a motion aftereffect (MAE) paradigm to generate depth from motion parallax. Following adaptation to a bi-directional motion stimulus, observers fixated a stationary test stimulus. With a stationary head, observers perceived the MAE, but when the head was translated from side-to-side observers perceived a motion parallax-like depth percept. In this paradigm, the motion signal provided by the MAE remained constant, but perceived depth reversed as a result of the reversal in observer head translation. One obvious source of a possible extra-retinal signal is the vestibular system. However, the stationary observer/translating monitor demonstration (Rogers & Graham, 1979) suggests that the vestibular system is not the source of the signal. A parsimonious explanation requires that the extra-retinal signal must be present for a stationary observer, therefore precluding the vestibular system from playing a direct role.

Because the extra-retinal signal must be available to both moving and stationary observers, the most reasonable source of the extra-retinal signal is the slow eye movement system (Nawrot, 2003a). Consider the paucity of extra-retinal cues available to a stationary observer who is instructed to maintain fixation on a translating stimulus. Therefore, the pursuit eye movement system is the obvious candidate for the source of the extra-retinal signal. Consistent with this eye movement hypothesis is the fact that many slow eye movement systems are very active when an observer moves. These eye movement systems compensate for the observer's body movement and stabilize a particular point of the scene on the observer's retina, thereby preserving visual acuity during body movement.

To maintain fixation on a particular point in space as the head is translated along the interaural axis, the eyes move in the opposite direction to, and 180 degrees out of phase with, the head movement. During these lateral head translations the main compensatory eye movement is the translational vestibulo-ocular response (TVOR) initiated by the vestibular organs (Angelaki, 2004). The TVOR, however, does not supply an extra-retinal signal for the perception of depth from motion parallax (Nawrot, 2003a, 2003b). In humans, at most viewing distances, the TVOR eye movement is smaller than what is required to maintain accurate fixation (Bussettini, Miles, Schwarz, & Carl, 1994). This means that a foveated visual target will have retinal slip that elicits a visually driven eye movement in the same direction as the TVOR. This visual backup to the TVOR has been referred to as the early component of the ocular kinetic response (OKRe) (Miles & Busettini, 1992; Miles, 1993). The OKRe helps maintain accurate gaze on the target and preserve acuity that would otherwise be compromised by the retinal slip produced by the under-compensating TVOR.

Consider also the compensatory eye-movements for a steadily translating observer, such as someone viewing out the window of an automobile (Gibson's "motion perspective"). Due to the sustained translation (no acceleration), the TVOR is not evoked. Instead, the observer fixates and tracks a specific point in the visual scene using pursuit eye movements alone. Therefore, all of the stimulus conditions that generate the perception of depth from motion parallax also generate visually driven, fixation-maintaining eye movements. However, are pursuit and OKRe eye movements the same?

While pursuit and OKRe show many similarities—maintenance of fixation, short time constant, no velocity storage, high acceleration and velocity, and sensitivity to disparity (Miles, 1993; Miles & Busettini, 1992)—these two terms may not refer to identical eye movement mechanisms. OKRe is believed to be the same mechanism as the ocular following response (OFR) (Kawano, 1999; Miles, 1998; Miles, Kawano, & Optican, 1986). The OFR is a reflexive "machine-like" open-loop eye movement phase having an ultra-short latency (<70–85 ms) (Kawano, 1999; Miles, 1998). In contrast, pursuit has longer latency and a less reflexive, more voluntary, nature. Moreover, discussions of neural mechanisms for OFR focus on cortical area MST (Kawano, 1999; Miles, 1998) while neural mechanisms for pursuit involve the smooth eye movement region of the frontal eye fields (Krauzlis, 2004). The most reasonable reconciliation is that the terms OKRe (OFR) and pursuit describe different aspects of an integrated process: OKRe describes the initiator phase that gets the eyes moving in the correct direction while pursuit describes the subsequent closed-loop maintenance phase that keeps the eyes on target. This is not an unlikely possibility because pursuit has both open-loop initiator and closed-loop maintenance phases (Morris & Lisberger, 1987) and OFR has been proposed as the initiating mechanism for visual pursuit (Kawano, 1999). During conditions of observer head translation, a pursuit signal is most likely generated in addition to the TVOR and OKRe. That is, to maintain accurate fixation over sustained head translations, a visually driven, closed-loop, fovea-specific, steady state eye movement phase (like pursuit) operates in addition to the OKRe. Furthermore, while it is known that pursuit is disrupted by ethanol intoxication, so are the visual-driven eye movements that serve as a backup to TVOR during observer head translation (Nawrot, Nordenstrom, & Olson, 2004). It is not known if alcohol intoxication affects the latency or gain of the ORF (OKRe). Indeed, perhaps our understanding of these eye movement systems may be aided by understanding their role in the perception of depth from motion parallax.

For these reasons, we propose to use the term "pursuit signal" to describe the extra-retinal signal provided by the eye movement system for the perception of depth sign when viewing a motion parallax stimulus. The next section outlines a simple model of how the direction of pursuit signal might be used in the human visual system to disambiguate the depth sign from motion parallax.

1.2. The pursuit theory of motion parallax

Given that a pursuit signal is generated in all of the conditions in which MP is found—with translational head movements, viewing out the window of moving vehicle, and when viewing a translating display—how does the visual system use the extra-retinal signal provided by the pursuit system? Nawrot (2003a) demonstrated a simple depth-sign rule based on the direction of the pursuit signal; retinal motion in the same direction as the pursuit signal is perceived farther away than fixation. Retinal motion in the opposite direction is perceived nearer than fixation. This is illustrated in Fig. 1, with the observer translating to the right and making a compensatory eye movement to the left. The bottom retinal image call-out illustrates that the image of object in near depth (cube) moves rightward on the retina. However, it is confusing to consider both the direction of eye movement and the direction of retinal motion, which is opposite the direction of perceived motion. Therefore, it is often easier to consider the depth-sign rule with respect to relative movement in the scene. In Fig. 1 the upper scene

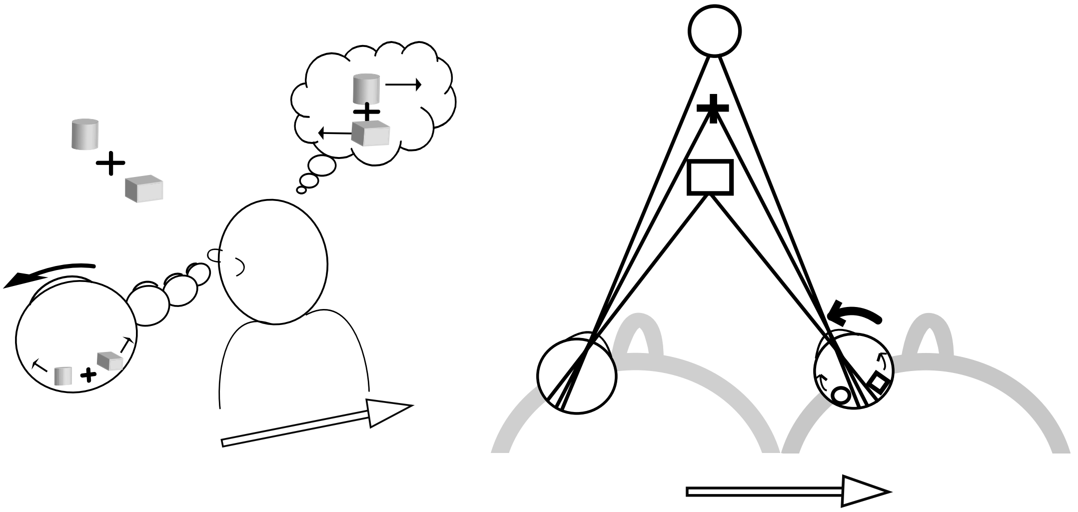

Fig. 1. Motion parallax is produced by lateral observer translation, shown here as movement to the right, while fixation is maintained on a specific object (the cross) among a group of stationary objects. In this case, as illustrated in the call-out above the observer's head, objects nearer than the fixation point (the cube) have relative motion in the direction opposite of the observers translation (leftward) and objects farther away than the point of fixation (cylinder) translate in the same direction as the observer (rightward). The relationship between relative depth and movement is opposite if we consider retinal motion, as illustrated in the eye-ball call-out. The right panel illustrates a geometric top view of the observer translation to right, and shows how the objects nearer and farther than the fixation point move on the observer's retina.

image call-out illustrates scene motion in the same direction as the pursuit signal is perceived nearer than fixation while scene motion in the direction opposite the pursuit signal is perceived farther away than fixation.

Nawrot (2003a) demonstrated the fallibility of an alternative rule based on head translation (Kitazaki & Shimojo, 1998) or TVOR eye movement direction. Moreover, when the pursuit signal is absent (but head and TVOR eye movements are still present), the perceived depth from motion parallax is depth-sign ambiguous (Ono & Steinbach, 1990; Nawrot, 2003a). While pursuit is crucial for the neural mechanism serving the perception of depth from motion parallax, this does not mean that head translation is irrelevant. Instead, outside the laboratory, it is only with observer translation that the parallax of objects is actually produced. However, with regard to the underlying neural mechanisms, the visual system does not appear to use a head translation signal. It is often assumed (erroneously) that the vestibular system could provide such a signal, but it is ill suited for this task. The vestibular system is sensitive to accelerations, not to steady translations. Therefore the neural processing mechanisms would be better served by an extra-retinal pursuit signal as a proxy for the direction of observer translation. Indeed, it is possible to manipulate this system in the laboratory, for example by moving the stimulus along with the observer's head translation, thereby reversing the direction of the pursuit signal and thereby reversing the perceived depth sign in the stimulus (Nawrot, 2003a). A version of this particular manipulation is included in the present experiments.

The pursuit theory of motion parallax also provides a mechanism to suppress perceived movement during conditions providing depth from motion parallax. Consider that a pursuit eye movement causes movement of stationary objects across the retina. However, this retinal motion is not interpreted as movement in the environment. This suppression of perceived motion is usually explained by the corollary discharge model (Teuber, 1960), in which an efferent copy of the eye movement command is compared to movement across the retina. One consistent problem with current explanations of motion parallax is the change in subjective experience of visual movement, which is instead perceived as depth. For instance, in the Ono and Ujike (1994) demonstration (see also Nawrot, 2003a) the perception of illusory motion due to the motion after-effect is completely nullified, and the relative motion is instead perceived as depth. The pursuit theory, relying on an extra-retinal pursuit signal, is likely participating in corollary discharge, while also providing a signal for depth in motion parallax.

Indeed, the pursuit theory represents a visual processing model where the perceptual outcome relies on a very early sensory/motor integration, not simply passive sensory processing. Neurons found in cortical areas MT and MST appear ideally suited to play a role (Upadhyay, Page, & Duffy, 2000; Bradley, Qian, & Anderson, 1995, 1998). Roy, Komatsu and Wurtz found many MSTd neurons displaying a reverse in direction selectivity as the motion moved between crossed and uncrossed disparity. The response was independent of vergence angle meaning these direction selectivities are relative to the fixation plane. They termed these disparity-selective, direction selective (DDD) neurons. Komatsu and Wurtz (1988a, 1988b) found that many MSTd neurons also receive an extra-retinal input regarding the direction of pursuit eye movements (neurons are active during pursuit in the dark) (Newsome, Wurtz, & Komatsu, 1988). It is not unreasonable to suppose that some MSTd neurons demonstrate a combination of properties required of the pursuit theory of motion parallax: depth-dependent, motion-dependent, pursuit-dependent response (near depth, motion direction = pursuit direction). Just as Bradley, Chang, and Andersen (1998) found MT neurons that fulfilled the predicted neural response properties predicted by the Nawrot and Blake (1991) model of kinetic depth effect, the work proposed here may provide the basis for the search for MT or MSTd neurons displaying this particular set of functional properties necessary for the pursuit model of motion parallax. Nadler, Angelaki, and DeAngelis (2005) have reported preliminary evidence that some MT neurons show a response selectivity that combines direction of motion with an extra-retinal signal for the possible coding of depth from motion parallax. This is evidence that MT neurons use a extra-retinal signal in the perception of depth from motion parallax.

The necessary addition to these neural network models (Nawrot & Blake, 1991; Bradley et al., 1998) could be as simple as adding direction-dependent facilitatory inputs from the pursuit system as illustrated in Fig. 2. The simplest version of this model (Bradley et al., 1998) uses four neural units, each exhibiting a unique combination of response selectivity to near or far depth, and leftward or rightward motion. Active units are shown in black, while inactive units are shown in grey. As illustrated in Figs. 1 and 2A, if the observer translates to the right and maintains fixation on the cross, the cube would move leftward in the scene and activate neural units selective to leftward motion. In contrast, the cylinder activates units selective to rightward motion. Because the motion itself is depth-sign ambiguous, both near- and far-units are activated by the object motion. However, depth-sign could be disambiguated by the facilitatory pursuit signal connections suggested in Fig. 2A. Consider that the rightward observer translation also generates a leftward pursuit signal (the condition illustrated in Fig. 1). Leftward pursuit provides a facilitatory input to units representing rightward motion in far depth, and leftward motion in near depth. The high activity of these units corresponds to the perception of the cube appearing near, and the cylinder appearing far in depth.

The same neural network, with the same set of connections, models the same depth percepts with observer translation in the opposite direction (Fig. 2B). With the reversal in head translation, the direction of object motion also reverses. This is illustrated in Fig. 2B by the cylinder activating units selective to leftward motion while the cube activates units selective to rightward motion. With the reversal in head translation comes a concomitant reversal in the direction of the pursuit signal. Facilitatory connections from a rightward pursuit signal, which were inactive in the conditions of Fig. 2A, are now active and provide a facilitatory input to units selective to rightward motion in near depth and leftward motion in far depth. With the facilitatory connections from rightward pursuit active, the neural units representing the cube at near and the cylinder at far depth are active. The output of the model, cube in near depth and cylinder at far depth, remains constant with reversal in observer translation, and changes in the neural units that are active. The pursuit driven activity in MST neurons studied by Komatsu and Wurtz (1988a, 1988b) suggest that this is a plausible model for the disambiguation of depth from motion in the conditions of motion parallax.

In addition to the neurophysiological predictions above, the pursuit theory generates many testable psychophysical hypotheses regarding eye movements and the perception of depth. For instance, the reduction of smooth pursuit gain with ethanol intoxication interferes with in the perception of depth from motion parallax (Nawrot et al., 2004). Also, while Thompson and Nawrot (1999) suggested the motion

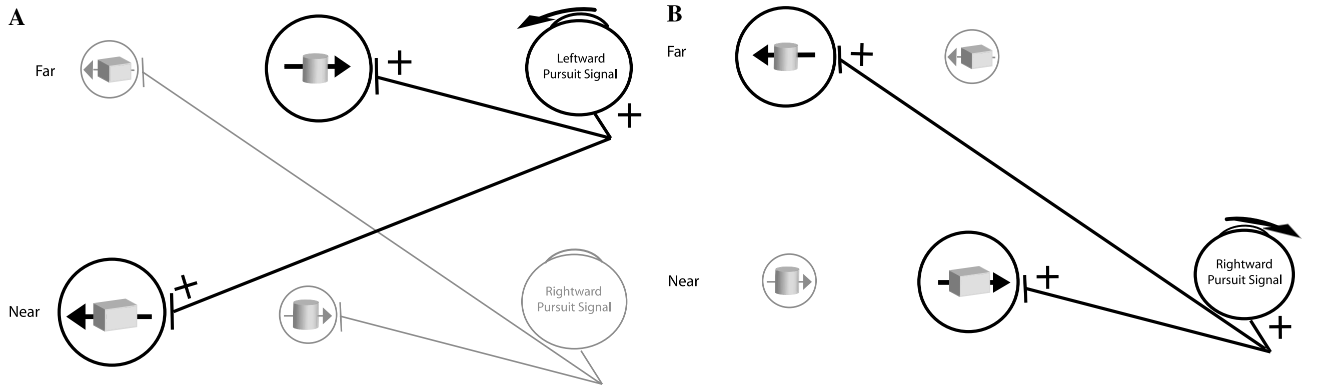

Fig. 2. Shown is a possible set of neural connections suggested by the pursuit theory of motion parallax. (A) The rightward translation of the observer in Fig. 1 would produce leftward motion of the cube and rightward motion of the cylinder. An extra-retinal signal provided by a pursuit system disambiguates the perceived depth of the two opposite motion signals (much like the connections suggested by Nawrot and Blake, 1991 and Bradley et al., 1998). In this case the leftward pursuit signal is active and the rightward pursuit inactive. The leftward pursuit signal provides a facilitatory input to leftward motion at near depth and rightward motion at far depth. (B) When the direction of observer translation reverses, the direction of the pursuit signal reverses (rightward pursuit becomes active) and the direction of the relative object motion reverses. The rightward pursuit signal provides a facilitatory input to rightward motion in near depth and leftward motion at far depth. The change in the activity of the relevant neural units results in the cube being perceived in near depth in both directions of observer translation.

parallax deficit with strabismus was due to a more general depth-processing problem, the pursuit theory suggests the deficit might be more specific and related to the pursuit asymmetry with esotropia (Demer & von Noorden, 1988; Westall et al., 1998). That is, temporo-nasal (TN) eye movements are normal while naso-temporal (NT) eye movements have a reduced velocity (quantified as gain). As predicted by the pursuit theory, the motion parallax deficit with esotropia is actually asymmetric and is found only in the NT pursuit direction (Nawrot, Frankl, & Stockert, 2004; Frankl & Nawrot, 2005). Esotropic observers with normal pursuit in the TN direction have normal motion parallax thresholds when moving their eye in the TN direction.

Overall, it appears that pursuit has an important role in the unambiguous perception of depth from motion parallax. The experiments presented below seek to demonstrate that the relationship between pursuit direction, direction of retinal motion and perceived depth is just as lawful as the relationship between sign of retinal disparity and perceived depth sign for stereopsis.

2. Methods

2.1. Apparatus

Stimuli were presented on a 17″ Sony Trinitron monitor with a 0.27 mm dot pitch, at a viewing distance of 47 cm (1 pixel = 2 min arc). The monitor face subtended an area of 38 × 29 deg. The monitor was driven by an ATI graphics board controlled by a Macintosh G4 computer. The computer interfaced with external devices through a multifunction I/O board with digital I/O and 16-bit ADC and DAC (National Instruments; Austin, TX). All programs for stimulus presentation and data collection were written with the Metroworks CodeWarrior integrated development environment (Freescale Semiconductor; Austin TX).

Observer head position was limited to translations along the interaural axis by a headrest affixed to a slide that moved smoothly and effortlessly (<1 N force) on linear bearings. A linear potentiometer (ETI Systems; Carlsbad CA), attached to the slide and interfaced through the multifunction I/O board, allowed head position to be determined with an accuracy greater than 0.01 mm, with a 22.5 cm stop-to-stop linearity greater than $r^2 = 0.999$. When required of the particular condition, observers made head translations between 0.5 Hz, (which observers felt was slow) and 1.0 Hz, (which observers felt was fast). Typical head translations were around the center 13 cm of the device's 22.5 cm total range.

Similar to lateral head translation of observers, the display monitor could be manually translated 47 cm laterally on a platform riding on linear bearings. Similar to the head movement device, a linear potentiometer allowed the position of the platform to be determined to the nearest 0.01 mm. The monitor movement device had a stop-to-stop linearity greater than $r^2 = 0.999$. The monitor was typically translated about 17 cm at a frequency of about 0.5 Hz.

In conditions 4 and 7, in which the observer had a fixed head position and viewed a fixed position on the monitor, a video based eye tracking system (Applied Science Laboratories; Bedford MA) was used to monitor the observer's point of fixation. Due to the sluggish dynamics, this recording system was unable to be used when the observer's head was translated. In the second experiment eye movements were measured with a head-mounted infrared limbus tracking system (Skalar; Delft, Netherlands). With infrared LED's this eye tracker allows eye tracking in complete darkness, while remaining invisible to the observer. Due to the difficulties of keeping this system well calibrated over an extended period of psychophysical data collection, including many observer head movements, this system was not used to monitor the point of fixation during the psychophysical data collection.

In the condition, stereo stimulus presentation used the frame-sequential technique with ferro-electric shutter glasses (DisplayTech; Longmont, CO). The shutters were mounted in metal trial frames. These shutters have a 1000:1 contrast ratio between on and off states, and can transition between the states in 70 μs. The shutters were controlled by a driver (DisplayTech; Longmont, CO), which received a digital output signal from the multifunction board in the computer. The high speed of the system and high occlusion of the shutters allowed no detectable cross-talk in the stimuli that were to be presented individually to each eye.

2.2. Stimuli

Identical random-dot motion parallax stimuli were used for all conditions in this experiment. The stimulus depicted three vertical cycles of a corrugated random-dot surface, undulating towards and away from the observer. This random-dot stimulus type excludes other pictorial sources of depth information while still generating vivid percept of depth from motion parallax (Rogers & Graham, 1979). The stimulus comprised 10,000 2 min × 2 min black dots drawn in randomly selected positions on a white background within a 13.3 × 13.3 deg stimulus window. The depth corrugation had a spatial frequency of 0.2 cyc/deg. A thin, 2 min black line delineated the top and bottom halves of the stimulus window, and a small fixation square was drawn at the center. The stimulus window was either centered on the monitor face, or translated laterally across the monitor, depending on the condition.

Similar to the original design of Rogers and Graham (1979), within the motion parallax stimulus window, individual dots were translated horizontally in relation to observer or monitor translation, reversing motion with the observer or monitor reversed direction. Dots representing peaks and valleys of the corrugation had the highest horizontal dot speeds (but in opposite directions) and with other dot velocities derived from a vertically oriented sinusoidal function. Dots lying on the horizontal midline always had zero velocity, signifying a zero crossing of the sinusoid. Perceived depth magnitude of the corrugations varied with peak dot velocity within the motion parallax stimulus window.

A unique set of five stimulus exemplars, having new dot positions, was created for each block of trials. For each trial one of these five stimuli was randomly selected for presentation. Finally, the direction of stimulus dot movement, which is a factor in the perceived phase of the stimulus, was randomly determined for each trial.

Most commonly, the motion parallax stimulus, when yoked to head translation, has been quantified using a comparison to binocular disparity called disparity equivalence (Nawrot, 2003b; Rogers & Graham, 1979). For instance, one minute of disparity equivalence means that a stimulus dot has translated one minute for a head translation the amount of the interocular distance (6.5 cm). This distance would move one eye to where the other eye would be for a binocular stereoscopic view of the stimulus. Similar to binocular stereopsis, larger disparity equivalence (larger dot translation) generates larger magnitude of perceived depth. However, in the current experiment the observer's head was often stationary and either the monitor or the stimulus window was translated. To allow comparisons between the various conditions in this experiment, the expression of disparity equivalence will also be made in reference to monitor or window translation, not only head translation.

2.3. Procedure

Observers were seated in a darkened room. A semi-circular headrest was provided. In some conditions the headrest was allowed to slide laterally allowing the measurement of head movements, while in other conditions the headrest was fixed, thereby constraining head position. In some conditions the entire monitor translated laterally while in other conditions the stimulus window moved on the monitor face (Fig. 3). In conditions 2 through 7 the observer viewed the stimulus monocularly, with an eye patch occluding the left eye. Trials began with a small fixation spot on a white screen. In every condition the observer was instructed to maintain

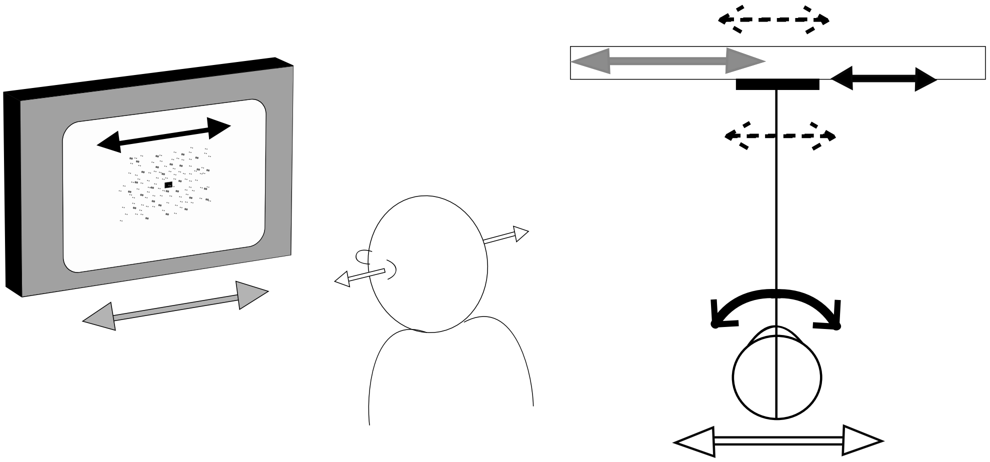

Fig. 3. In the general design of the experiment, the observer can translate laterally (open arrows), the monitor can translate laterally (grey arrow) and the stimulus window upon the monitor face can translate laterally (black arrow). In every condition the small stimulus dots translate within the larger stimulus window. The fixation dot remains fixed within, and translates along with, the stimulus window. The right panel shows a top view of the experimental variables. The eye-ball (open arrow) depicts observer translation while the curved arrow depicts the direction of the pursuit signal. The open rectangle (and grey arrow) represents the monitor translation, and the smaller black rectangle (black arrow) represents the stimulus window translation. The dotted arrows represent the direction of stimulus dot movement predicted by the pursuit theory to be perceived nearer or farther in depth.

fixation on the spot at the center of the stimulus, regardless of whether the stimulus window, the monitor, or the observer moved in that condition. Following fixation of the spot, the observer initiated stimulus presentation with a key press. The stimulus was presented for unlimited viewing, although observers typically made a key-press response within a few seconds, which terminated the stimulus presentation. The observer's task was to perform a depth-phase judgment of the stimulus. That is, observers reported which half-cycle of the depth corrugation, immediately above or below the fixation point, appeared father away in depth.

Using a staircase procedure to determine thresholds (Wetherill & Levitt, 1965), this phase discrimination task was implemented as a test of the pursuit theory of motion parallax. That is, dots within the stimulus half-cycle that moved in the direction opposite the direction of the observer's pursuit signal should be perceived as farther than the fixation point. For example, if the stimulus half-cycle (with dots moving in the direction opposite the observer's pursuit signal) lay immediately below the fixation spot, the correct response was that the bottom or lower half of the stimulus was farther away. The staircase procedure was used to find the minimum amount of stimulus dot movement for which observers responded in accordance with the pursuit theory of motion parallax. The staircase procedure began with 20 min of disparity equivalence. The staircase ended when it reached floor (1 min disparity equivalence, or 2 min, a single pixel, in the case of binocular disparity), the ceiling (78 min of disparity equivalence), or after 13 reversals of the staircase. In the first two cases, the ceiling or floor value was taken as an estimate of the observer's threshold. In the case of the procedure ending on reversals, the observer's threshold was determined from the average of the last 10 reversals.

Six observers, two authors and 4 naïve volunteers, participated in the experiment. Each observer completed three blocks of trials in each of the conditions. From this a mean threshold value was determined for each observer, and for the entire condition.

3. Experiment 1

3.1. Condition 1—binocular stereopsis

A stereoscopic version of the stimulus was used to both familiarize observers with the depth-phase task and to serve as a non-motion parallax control condition for this experiment. Observers wore the shutter glasses and viewed the stimulus binocularly. The observer's head, the monitor, and the stimulus window remained stationary. Performance in this condition is based solely on the use of binocular disparity information for depth.

3.1.1. Results

As expected, perceived depth when viewing the stereoscopic stimulus was unambiguous. The stimulus half-cycle with dots presenting crossed disparity was always perceived nearer than the fixation point. Observers had no difficulty reporting the correct depth phase with even the smallest magnitude of stimulus disparity. All observers took the staircase procedure down to the floor of 2 min (mean = 2, SE = 0.0).

3.2. Condition 2—head translation

This motion parallax condition required the observer to make lateral head translations while viewing a motion parallax stimulus (Fig. 4). The monitor and stimulus window remained stationary. Observer's were instructed to maintain fixation on the stationary fixation point while making the head translations. Stimulus dots moved in relation to observer head movement. The eye movements generated in this condition are a combination of the vestibularly-driven TVOR and visually-driven OKR and pursuit.

3.2.1. Results

Similar to the original report by Rogers and Graham (1979), perceived depth when viewing this motion parallax stimulus was unambiguous. Observers had no difficulty reaching the floor with the staircase procedure (mean = 1 min, SE = 0.0). In line with the pursuit theory of motion parallax, the stimulus half-cycle with dots moving in the same direction as the pursuit signal was always perceived nearer than the fixation point while the stimulus

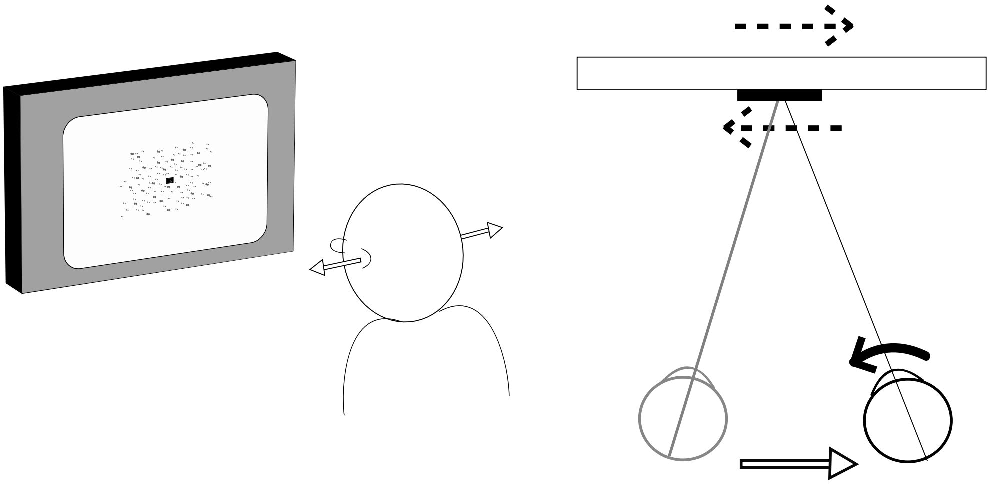

Fig. 4. In condition 2 the observer translates from side-to-side, while the monitor and stimulus window remain stationary. When the observer translates to the right, the pursuit signal is to the left, and leftward moving stimulus dots should be perceived near in depth.

half-cycle with dots moving in the opposite direction was perceived as farther than fixation.

3.3. Condition 3—monitor translation

If observer head translation is not used to determine depth sign in motion parallax, then the removal of head translations should not affect the unambiguous perception of depth sign in motion parallax. The current condition is similar to Rogers and Graham's (1979) external parallax conditions, wherein a stationary observer viewis a monitor translating in a 57 cm radius arc. Rogers and Graham reported condition produced an unambiguous depth percept, but the perceived depth magnitude was less than with observer head translations.

The current conditions employ a linear translation of the monitor rather than an arc (as in Rogers & Graham, 1979) or a head translation as in the previous condition (Fig. 5). Here the experimenter translated the monitor laterally about 17 cm at a frequency of about 0.5 Hz. With this monitor movement, the fixation spot, stationary upon the monitor face, moved about 20 deg. Dots within the stimulus window sheared in relation to the monitor movement, much as they had in the condition of observer translation, allowing the computation of disparity equivalence by replacing head translation with monitor translation. Observers were instructed to maintain fixation on the moving monitor using pursuit eye movements. If the pursuit theory is correct, stimulus dot moving within the stimulus window in the same direction as the monitor translation should be perceived near in depth.

3.3.1. Results

Perceived depth in this condition was unambiguous. Stimulus dots translating in the same direction as the monitor translation were perceived nearer than fixation point. The mean threshold for the six observers was 1.25 min DE (SE = 0.44), with most trials ending with the staircase reaching the floor of 1 min DE.

If head movements were a crucial aspect in the disambiguation of depth from motion parallax, the observers should have had difficulty performing the task in such a reliable

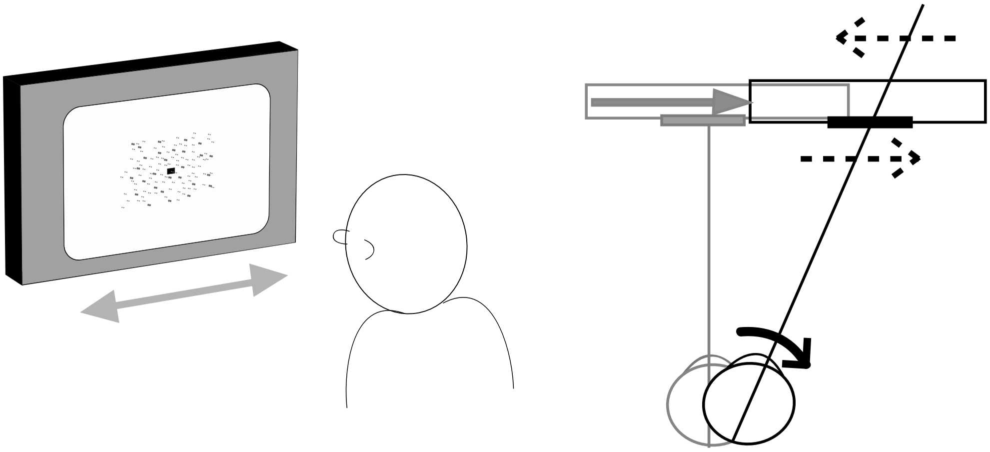

Fig. 5. In condition 3 the monitor is translated from side-to-side. The observer is stationary. A rightward moving monitor will elicit a rightward pursuit signal. Rightward moving stimulus dots should be perceived nearer in depth.

manner. Instead, this result is consistent with the depth interpretation predicted by the pursuit theory. Movement of the fixation point upon the monitor face elicited pursuit eye movements in the same direction as monitor translation, and therefore served to disambiguate perceived depth in this stimulus. This result confirms similar findings by Rogers and Graham (1979), Nawrot (2003a) and Naji and Freeman (2004) that head translations are not required for the unambiguous perception of depth from motion parallax.

3.4. Condition 4—stimulus window translation

If monitor translation is sufficient to elicit a pursuit eye movement and produce an unambiguous percept, so too should translation of the stimulus window upon the monitor face. In a design similar to the third condition of Naji and Freeman (2004), both the observer's head and the monitor remained stationary while the stimulus window translated across the monitor face at a speed of 15 deg/s (Fig. 6). The stimulus window translated 15 deg across the monitor face with a frequency of 0.5 Hz. Again, observers were instructed to maintain fixation on the fixation point at the center of the moving stimulus window.

3.4.1. Results

These viewing conditions produced unambiguous perception of depth from motion parallax. Similar to the previous condition, stimulus dots moving in the same direction as the observer's pursuit eye movements were perceived nearer than the fixation point. The mean threshold was 1.07 min DE (SE = 0.22) with most blocks ending at the staircase floor of 1 min. This result illustrates that head movements are not required for the unambiguous perception of depth from motion parallax.

3.5. Condition 5—no translation

If a pursuit signal provides to the visual system the information required to disambiguate the perception of depth from motion parallax, then the removal of eye movements should cause the stimulus to become depth-sign ambiguous. In this condition the observer's head, the monitor, and the stimulus window all remained stationary. This was implemented by using the same stimulus presentation program written for the previous condition, with the exception that the stimulus window translated at zero velocity and therefore was always drawn at the center of the monitor. All other aspects of the program remained unchanged. The program still used the assigned direction of stimulus window translation (with zero speed), to determine whether a response was "correct" or not. Of course, with the stationary stimulus window, and stationary fixation point, there should be no eye movements elicited (Fig. 7), and in the absence of a pursuit signal the stimulus is expected to depth-sign ambiguous. Observers maintained stable fixation (verified with an eye tracker during pilot testing) despite the translation of the stimulus dots in opposite directions on either side of the fixation point.

3.5.1. Results

Perceived depth was depth-sign ambiguous in this condition. Some observers reported that the stimuli were perceptually bi-stable, in which case observers were asked to make a response based on their first percept of the stimulus. Most blocks ended at the staircase ceiling of 78 DE, although some trials ended with reversals while moving towards the staircase ceiling (mean = 68 min DE, SE = 3.7). This condition is similar to second condition of Naji and Freeman (2004) who also reported that the stimulus was depth-sign ambiguous in the absence of pursuit. While Naji and Freeman reported a slight perceptual preference for the stimulus region above the fixation point to be nearer in depth, the current experiment found a slight bias for observers to perceive the stimulus region above the fixation point as farther away in depth (mean 57%, range 48–70%). This most likely reflects individual differences of the observers in the two studies. Overall, the result of this condition demonstrates that the motion par-

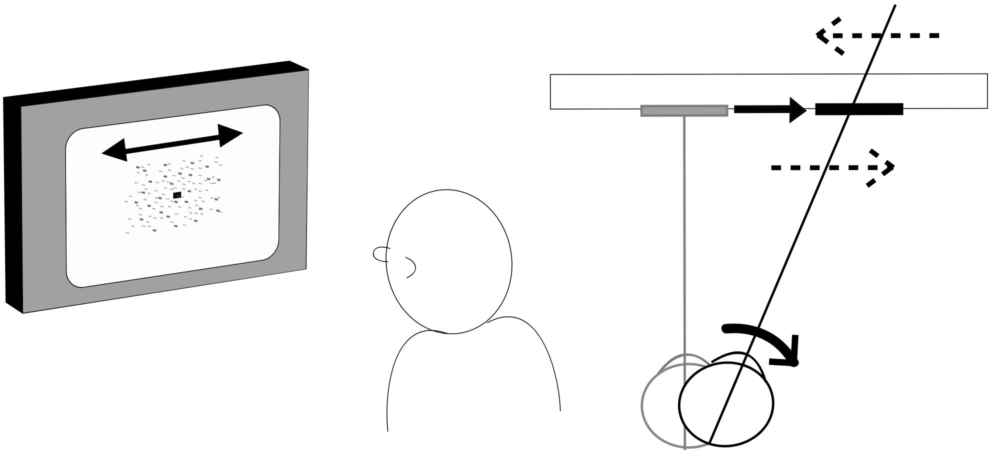

Fig. 6. In condition 4 the stimulus window translates from side-to-side across the monitor face. The monitor and the observer are stationary. A rightward moving stimulus window will elicit a rightward pursuit signal. Rightward moving stimulus dots should be perceived nearer in depth.

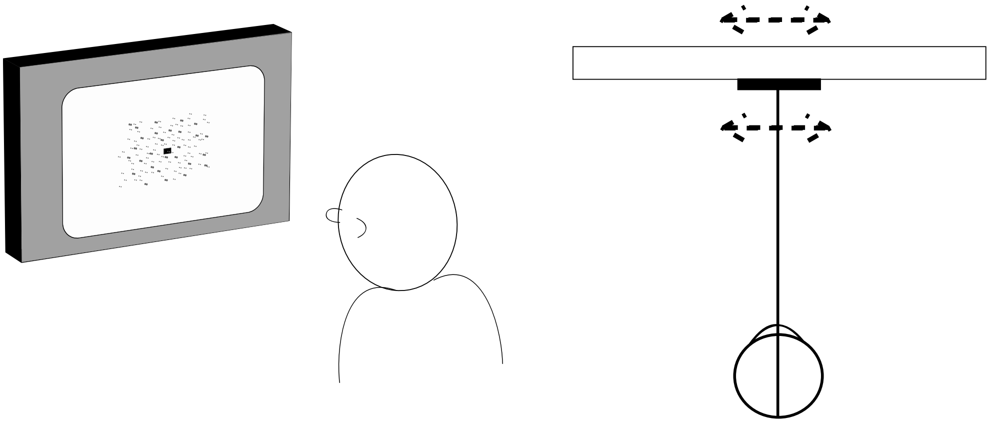

Fig. 7. In condition 5 the stimulus window, the monitor, and the observer are stationary. The stimulus dots translate within the stimulus window. No pursuit signal is elicited. The stimulus should be depth-sign ambiguous with either leftward or rightward dots appearing nearer in depth.

allax stimulus is depth-sign ambiguous in the absence of a pursuit signal.

3.6. Condition 6—synchronized head and stimulus window translation

While a pursuit signal appears to be inextricably linked to the perception of depth from motion parallax, it remains to be determined whether a head movement signal alone could possibly serve a similar role. For instance, Ono and Ujike (2005, see also Ujike & Ono, 2001) link the perception of depth from motion parallax to observer head movement velocity and derive an interesting, but perhaps indirect, parameter space for motion parallax. However, if the visual system is relying on an eye movement signal instead of a head movement signal, it is less clear what this parameter space is telling us about the neural mechanisms serving motion parallax. This concentration on head movements in motion parallax is partially due to the difficulty in separating the roles of eye and head movements. They most often co-vary in the conditions that produce motion parallax. While conditions 3 and 4 attempted to isolate the pursuit system, it is not as simple to isolate the effects of head translation. For instance, one might attempt to isolate the effects of head translation by linking the stimulus window position to the observer's head translation. As the observer translates, the stimulus window translates across the monitor face in phase with the observer. If the observer's task is to maintain stable fixation in the center of this stimulus window, then the observer's eye remains stationary in the orbit (e.g., Nawrot, 2003a).

However, during an abrupt head translation a TVOR is generated, which moves the eyes in the direction opposite the head translation. To overcome the TVOR, and maintain fixation on the target moving with the observer's translation, the visual system must generate a pursuit eye movement in the same direction as the head movement. Even thought the eye remains stationary in the orbit, within the visual system both TVOR and pursuit signals are being generated. Previous work (Nawrot, 2003a) has shown that this TVOR-canceling pursuit signal is sufficient to disambiguate the perceived depth in a motion parallax-like display. The perceived depth-sign results in that condition suggested that it is the visually driven eye movement signal, not the TVOR, which serves to disambiguate depth from motion parallax.

The current condition used the same technique as Nawrot (2003a) to further investigate the role of pursuit and head movement/TVOR signals in a random-dot motion parallax display. Here, the stimulus window translated on the monitor face along with the observer's head translation (Fig. 8). The monitor itself remained stationary. The observer's task was to maintain fixation on the small square at the center of the stimulus window and report perceived depth phase of the stimulus. Responses for the staircase procedure were based on the depth phase predicted by the pursuit theory.

It is important to consider that movement of the stimulus window reverses the relationship between the direction of head translation and the direction of the pursuit signal seen in condition 2, generating opposite predictions for perceived depth sign. In condition 2, stimulus dots moving in the direction opposite the head translation were perceived nearer than fixation. If a head translation (and concomitant TVOR) signal is used to disambiguate depth sign in motion parallax, then stimulus dots moving in the direction opposite the head translation should be perceived nearer than fixation in the current condition. With regard to the direction of the pursuit signal, in condition 2 stimulus dots moving in the same direction as pursuit were perceived near. If the pursuit theory is correct, the same relationship will be found here, and the relationship based on the direction of head translation will fail. If signals are provided by both head translation and pursuit, these signals would now be in conflict, and perception might show some indication of being depth sign ambiguous.

3.6.1. Results

Perceived depth sign of the stimulus was unambiguous, and was consistent with the pursuit theory of motion parallax. Observers had no difficulty performing the depth phase judgment and most blocks ended when the staircase reached the floor of 1 min (mean = 1.5 min DE, SE = 0.3).

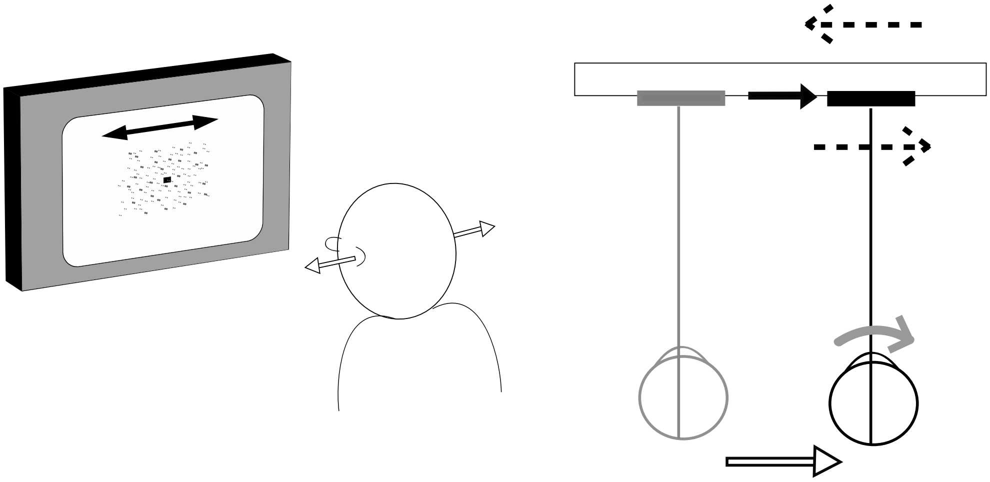

Fig. 8. In condition 6 the stimulus window moves along with the observer's head translation. A rightward head translation elicits a leftward TVOR that must be cancelled with a rightward pursuit signal so that fixation can be maintained on the rightward moving stimulus window. The result is a eye that remains fixed in the orbit, but a rightward pursuit signal available to the visual system. Therefore, rightward moving stimulus dots should be perceived nearer in depth.

This means stimulus dots moving in the same direction as the pursuit signal were perceived near in depth. This is the same relationship demonstrated in condition 2. However, with regard to the direction of head translation, the perceived depth is reversed in this condition compared to condition 2. That is, the identical head translation generates opposite percepts depending on whether the stimulus window remains stationary or it moves along with the observer. This result means that the visual system does not use the direction of head movement to disambiguate the perception of depth from motion parallax.

3.7. Condition 7—opposite monitor and stimulus window translation

The final condition replaced the observer head translation of condition 6 with monitor translation, similar to condition 3. As the monitor translated from side-to-side the stimulus window moved in anti-phase on the monitor face, remaining stationary relative to the world and relative to the stationary observer (Fig. 9). Although the experimenter avoided translating the monitor farther than the stimulus window could translate upon the monitor face, the stimulus window was extinguished if it reached the edge of the monitor face. The observer's eyes remained stationary on the stationary fixation point (relative to earth coordinates) as observed with a video based eye tracker. Because this condition had no head translations, and no TVOR, one hypothesis was that no pursuit signal would be generated, and perceived depth would be ambiguous, just as was found in condition 4. The alternative hypothesis was that translation of the monitor would induce reflexive optokinetic eye movements. To explore this hypothesis, eye movements were first measured when observers viewed a blank translating monitor with the instructions to keep their gaze straight ahead (Fig. 10A). Translation of the monitor was

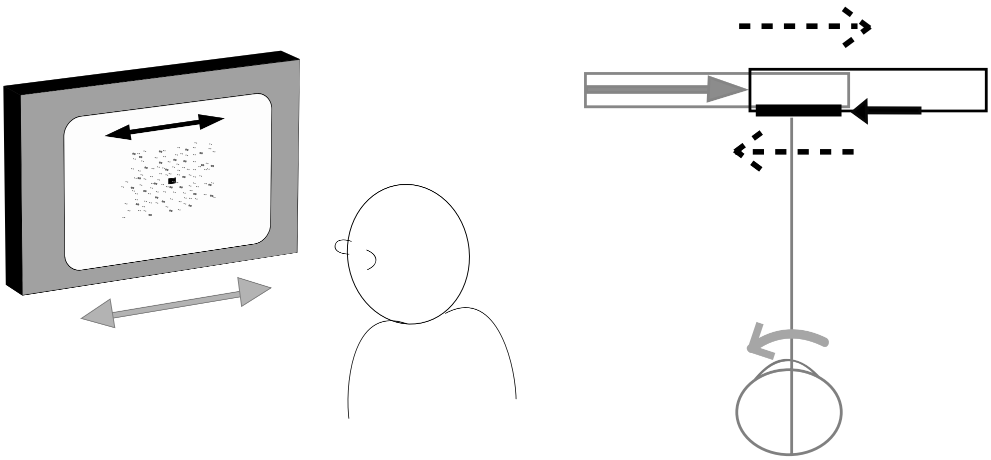

Fig. 9. In condition 7 the stimulus window translates in anti-phase to the monitor as it translates from side-to-side. A rightward moving monitor elicits a rightward OKR that must be suppressed by a leftward pursuit signal. Although the eye remains fixed in the orbit, the leftward pursuit signal means that leftward moving dots should be perceived nearer in depth.

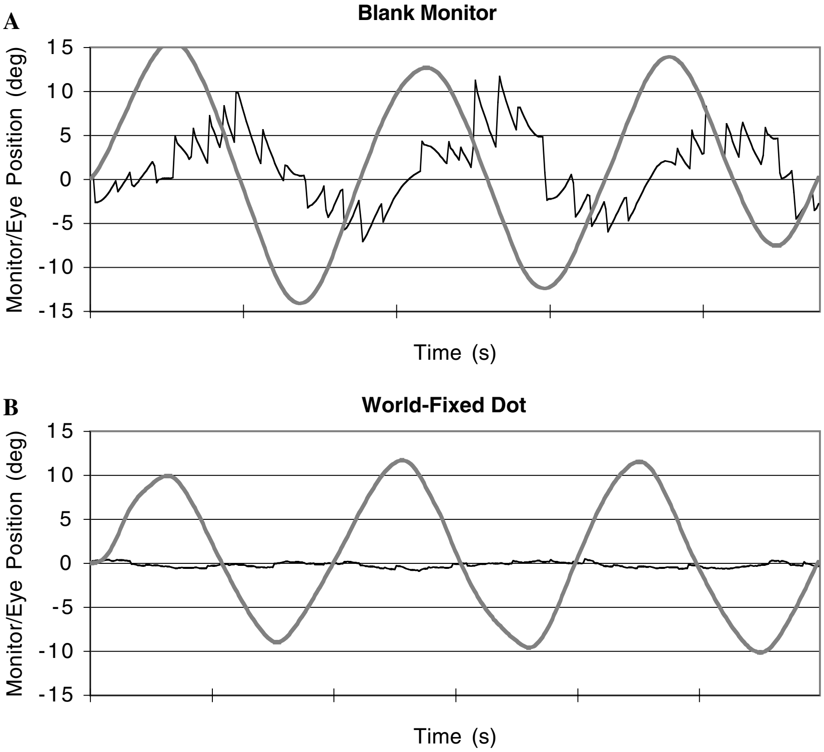

Fig. 10. (A) Eye movement recordings made when an observer viewed a blank monitor translating side-to-side. Horizontal eye (black) and monitor (grey) position is shown on the vertical axis and time is shown on the horizontal axis. Eye position exhibits optokinetic nystagmus with the slow phase in the direction of monitor translation. (B) Eye position with a world-fixed fixation point drawn on the monitor. The monitor moves from side-to-side, but the eyes remain stationary. In this case the visual system must use a countermanding pursuit signal to overcome the reflexive OKR elicited by monitor translation.

sufficient to elicit robust optokinetic nystagmus (OKN). This result is not surprising as movement in the peripheral visual field is known to elicit OKN (Abadi, Howard, Ohmi, & Lee, 2005; Cheng & Outerbridge, 1975; Howard & Ohmi, 1984). Moreover, observers could suppress this OKN with a countermanding pursuit signal when a world-fixed dot was drawn on the screen (Fig. 10B). Again, this is not surprising considering the evidence for linear summation of signals from pursuit and OKR and where pursuit dominance (especially in human) might be explained by higher internal gain values (Schweigart, Maurer, & Mergner, 2003). Therefore, in this condition a pursuit signal is available to disambiguate the perception of depth in the stimulus. Moreover, the pursuit signal should be in the direction opposite the monitor translation meaning dots moving in the direction opposite the monitor translation should be perceived in near depth.

3.7.1. Results

Perceived depth in this condition was unambiguous, although observers required an average of 4.5 min DE (SE = 0.8) to reliably perform the depth phase judgment. As for perceived depth-sign, stimulus dots moving in the direction opposite the monitor translation were perceived nearer in depth. If the pursuit theory is correct, this means that a pursuit signal was being generated in the direction opposite the direction of monitor translation. This the outcome predicted above. This explanation is consistent with the idea of “optokinetic potential” (Post & Leibowitz, 1985; Sumnall, Freeman, & Snowden, 2003). That is, translation of the monitor generated a reflexive OKR eye movement. To maintain fixation, a pursuit signal is generated to cancel or suppress the OKR (Post & Leibowitz, 1985). This pursuit signal, although not expressed as an overt eye movement, is used within the visual system to disambiguate the perception of depth from motion parallax. Further support for this “optokinetic potential” explanation comes from a set of studies by Nawrot and Stockert (2005) who used a stationary monitor and a translating OKR grating surround. This OKR grating surround was sufficient to disambiguate the perception of depth from motion, even when the observer’s eye remained stationary.

A further demonstration of the importance of the direction of the pursuit signal comes from pilot testing of this condition in which the stimulus window failed to blank when it reached the edge of the monitor. Since the stimulus window could no longer translate across the monitor and remain world-fixed, the stimulus window began moving with the monitor. An observer fixating the center point is required to initiate pursuit in the opposite direction—the direction of monitor translation. In this instant the depth phase of the stimulus immediately reverses. When the monitor reverses, and the stimulus window again moves antiphase to the monitor and becomes stationary relative to the observer, the perceived depth phase again changes to reflect the change in the direction of the pursuit signal. This illustrates that any manipulation affecting the direction of the pursuit signal subsequently affects the perceived depth sign in motion parallax, and provides more evidence supporting the pursuit theory of motion parallax.

3.8. Conclusions from Experiment 1

The pursuit theory of motion parallax provides a single parsimonious explanation for all of the results in this experiment. Although the various stimulus conditions included head translations, monitor translations, and stimulus window translations, perceived depth sign was determined solely by the direction of the pursuit signal required to maintain stable gaze on the fixation point at the center of the stimulus window. In the second condition the observer's head translated, and fixation was maintained at the center of the stationary stimulus window. With the pursuit signal in the direction opposite the direction of head translation, stimulus dots perceived near in depth were those moving in the direction opposite head translation (but in the same direction as the pursuit signal). However, in condition 6 the stimulus window translated in synchrony with the observer's head translation. To maintain fixation at the center of the stimulus window a pursuit signal is now generated in the same direction as the observer's head translation. The perceived depth is reversed. Stimulus dots perceived in near depth are those moving in the same direction as the observer's head (but still in the same direction as the pursuit signal).

Most notably, observer head translation is not required for, nor is it determinative of, perceived depth sign in motion parallax. Certainly, head translation is an important component of the stimulus conditions that typically give rise to motion parallax, but these results show that the visual system does not directly monitor the direction of observer head translation. Instead, the visual system appears to monitor the direction of the pursuit signal. The next experiment presents a further demonstration that depth sign from motion parallax depends on the direction of pursuit signal, not on head translation.

4. Experiment 2

The previous experiment demonstrated that the direction of the observer's internal pursuit signal determines the depth sign in motion parallax. Perceived depth sign is not directly related to the direction of head translation. This is obvious from the opposite depth percepts reported in conditions 2 and 6, even though the head movement and retinal stimulus was identical in both conditions. Instead, the difference in the direction of pursuit signal produced the perceived change in depth sign. Of course, an interesting question is the phenomenology of the transition between the two opposite depth percepts in the parameter space between the limits represented by these two conditions. That is, what is the perceived depth sign when the stimulus window translates as some proportion of observer head translation? It there a sharp transition suggesting that only the direction of the pursuit signal is important, or a smooth transition suggesting a role for both the direction and magnitude of the pursuit signal. Moreover, does the perceptual crossover point have a relationship to the pursuit component of the compensatory eye movement?

Nawrot (2003a) pursued a similar question using the motion parallax /motion aftereffect paradigm developed by Ono and Ujike (2001). Nawrot (2003a) attempted to assess depth from motion parallax at the specific point where the pursuit signal would be absent. This point was determined by measuring the difference between the compensatory eye movements measured in complete darkness (TVOR alone—dark gain) and compensatory eye movements with a visible, stationary, target (TVOR and pursuit—light gain). In light conditions the compensatory eye movements were accurate, meaning a gain very close to 1.0. In dark the compensatory eye movements are much less than what is required to maintain the point of gaze on the (now invisible) target. In the dark, Nawrot (2003a) found the TVOR gain to be about 0.8 at a viewing distance of 57 cm and a head translation rate around 0.5 Hz. Using these estimates of the TVOR and pursuit components, the test stimulus was translated along with the observer's head at a gain of 0.2, negating the need for a visually driven pursuit signal to maintain fixation. In these conditions, the depth sign of the stimulus was perceptually ambiguous.

The current experiment further investigates the ambiguity in perceived depth sign resulting from the removal of the pursuit signal from the motion parallax viewing conditions. This perceptual ambiguity should be found in the parameter space between the limits of the stationary stimulus in condition 2 and the translating stimulus in condition 6. In both conditions the observer's head was translating side-to-side which should generate the same vestibularly driven TVOR eye movement. The difference between these two conditions is the direction of the pursuit eye movement evoked by the movement of the stimulus window. By varying the ratio of stimulus window movement compared to observer head movement, it should be possible to determine how perceived depth sign becomes ambiguous and then reverses depending on the pursuit signal.

4.1. Psychophysical procedure

This experiment employed the same random-dot motion parallax stimulus used in the previous experiment. In all trials observers made side-to-side head movements in time with a brief computer-generated click sound occurring every 500 ms. The magnitude of depth portrayed in the stimulus was fixed at 10 min DE at the viewing distance of 47 cm. The precise stimulus presentation was governed by the ratio of stimulus window translation in comparison to observer head translation. A ratio of 0 signifies a stationary stimulus window (e.g., condition 2 in the previous experiment). A ratio of 1 signifies a stimulus window moving along with observer head translation (e.g., condition 6 in the previous experiment). In the current experiment this stimulus window translation ratio varied in 7 steps between 0.2 and 0.8 using the method of constant stimuli. As in the previous experiment, the depth phase presented in the stimulus (e.g., direction of stimulus dot movement) was varied between trials.

Each of 6 observers completed 3 blocks of 112 trials. Observers wore an eye patch over their left eye. Observers initiated each trial with a key press. Observers were instructed to translate their head from side-to-side with each of the regular clicks from the computer, and to maintain gaze on the fixation point at the center of the stimulus, regardless of how much or how little the stimulus moved in that particular trial. The observer's task was to report the perceived depth phase of the stimulus with a key press on the computer keyboard.

4.1.1. Psychophysical results

Fig. 11 shows the proportion of responses for which the stimulus dots translating in the direction opposite the direction of observer translation were perceived nearer than the fixation point. Each of the different symbols corresponds to an individual observer. The smooth line corresponds to cumulative psychometric function fit to the data from all of the observers using an error function (erf) to generate the best approximation to the cumulative normal.

From these results it is clear that perceived depth phase varies dramatically depending on the ratio of stimulus window movement. At low stimulus window movement ratios (e.g., 0.2–0.3), stimulus dots moving in the direction opposite observer translation are most often perceived near. This is similar to stationary stimulus window results found in condition 2 above. However, at high stimulus window translation ratios (e.g., 0.7–0.8), stimulus dots moving in the direction opposite observer translation are most often perceived far. This is similar to the results found with a synchronous stimulus window in condition 6 above. The most interesting result is the smooth transition in the probability of reporting either of the two opposite perceptual states suggesting that the perception of depth sign becomes ambiguous with stimulus window translation ratios between 0.4 and 0.6. From the cumulative psychometric function the point of perceptual ambiguity ($p = 0.5$) falls at a stimulus window translation ratio of 0.55. The psychometric functions of individual observers fall in a range of stimulus window translations between 0.46 (observer signified by the open circles) and 0.60 (observer signified by the diamonds) with a mean of 0.54 (SE = 0.02) meaning that all of the observers show similar perceptual changes.

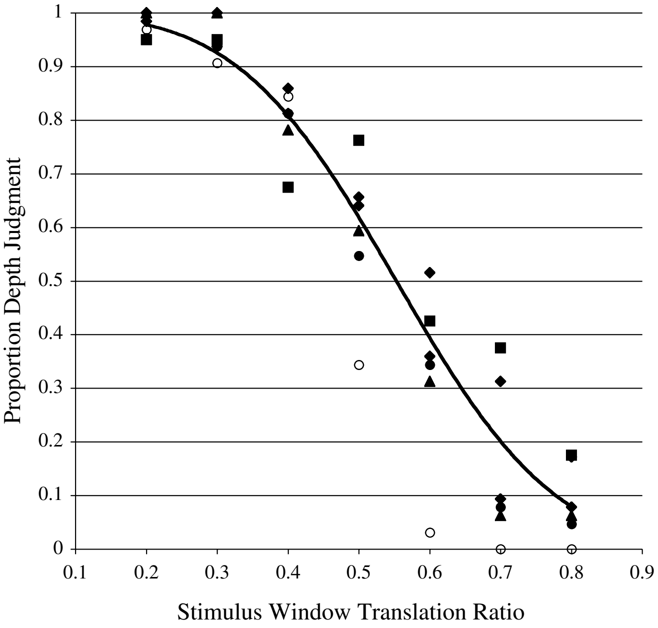

Fig. 11. Shown are the data points for each of the six observers and a global psychometric function fit to the cumulative data. The ratio of stimulus window movement to observer head movement is shown along the horizontal axis. The proportion of trials in which observers judged in near depth the stimulus dots translating in the direction opposite observer translation is shown on the vertical axis.

Phenomenologically these points mark an important transition between the likelihood of two opposite perceptual states. However, with regard to the pursuit model, this point should indicate a change in the direction of the pursuit signal. For a stimulus translation ratio lower than this point, pursuit is in the direction opposite head translation while for a stimulus translation ration higher than this point, pursuit is in the direction of head translation. This would explain the change in perceptual state. Of course, it is important to assess the eye movement components in these viewing conditions.

4.2. Eye movement procedure

If the pursuit theory is correct, the stimulus window translation that created perceptual ambiguity for this stimulus does so by the minimization of the pursuit signal. That is, when the TVOR alone adequately maintains fixation, then the pursuit signal should be absent and perception of depth from motion parallax should be ambiguous. The psychophysical data above suggest that this point of perceptual ambiguity is found near a window translation ratio of 0.55, and the pursuit component of the compensatory eye movement should be near zero at this point.

To independently assess the visual and vestibular components of the compensatory eye movements for this head translation speed and this 47 cm viewing distance, the eye movement recording procedures detailed in Nawrot (2003b) were used. Briefly, compensatory eye movements were recorded for head movements when a target was visible (light gain) and also in complete darkness with an invisible but remembered target (dark gain). The eye movements in the light gain conditions are a combination of both visual and vestibular (TVOR + pursuit) components. In dark conditions the compensatory eye movements are driven by the vestibular system alone. Subtracting the dark gain from the light gain yields an estimate of the pursuit component of the compensatory eye movement.

Following a calibration procedure, observers were instructed to translate their head back and forth in time with a computer generated click sound occurring every 500 ms. The observer was asked to maintain fixation on a small stationary spot at the center of a blank screen. The first 8 s trial recorded eye and head movements when the fixation spot was visible. For the second 8 s trial the monitor was extinguished and draped with black felt leaving the room completely dark. Observers immediately performed the same head translation task, maintaining fixation on their now remembered position of the fixation spot. Both eye position and head position were recorded at 75 Hz using the ADC in the experimental computer. Eye position was recorded from the right eye using the head-mounted infrared limbus tracking system (Skalar; Delft, Netherlands) while the left eye was occluded during testing.

4.2.1. Eye movement results

Details of the analysis procedure are given in Nawrot (2003b). First, only trials with linear calibration data ($r^2 >= 0.97$) were included in the analysis. This was greater than 80% of the recordings. Some trials had poor calibration due to the observer blinking while the calibration points were being recorded or poor positioning of the eye-tracking headset. For each of the light and dark recordings head position data were converted into expected eye position data in degrees left and right of center. Similarly, using the calibration data, the eye position data were converted to actual eye position in degrees left and right of center. Gain values were determined by comparing the actual and expected eye position for the central flat region of the translation, avoiding the extreme sections when the head and eyes were slowing and reversing direction. Subtraction of the dark gain from the light gain yields the visually driven pursuit component of the compensatory eye movements. The average pursuit component for the 6 observers was 0.57 (SE = 0.03) (the individual estimates from the psychophysical task and the pursuit task are similar, but the individual variability in the two tasks not significantly correlated, $r = 0.69$, $p > 0.05$). As expected, the pursuit gain values are similar to the perceptual cross over point in the psychophysical data, underscoring the link between pursuit and perceived depth sign in motion parallax. To explain, with a stimulus window gain value around 0.57 (in these particular movement and stimulus conditions, which differed from Nawrot, 2003a, 2003b) the pursuit system would not be engaged to maintain accurate fixation, TVOR could fulfill the task on its own, but only at this particular stimulus window gain value. At lower stimulus window gain values, pursuit would be required in the direction opposite observer translation. At higher stimulus window gain values, pursuit would be required in the same direction as observer translation. The ratio of stimulus window translation therefore determines the direction of pursuit, and perceived depth sign.

4.3. Conclusion

This experiment further demonstrates that perceived depth sign changes with the direction of the observer's extra-retinal pursuit signal. Moreover, when this pursuit signal is small or absent, perceived depth is ambiguous. The eye movement recordings provide further evidence that the perceived depth sign ambiguity was found at the point when the pursuit signal would have been at its minimum. The pursuit theory of motion parallax explains both the reversal in perceived depth sign and also the particular point of the perceptual reversal.

The smooth transition between these two states suggests that much more is needed to fully understand of the role of pursuit in the perception of depth from motion parallax. For instance, if the visual system relied solely on the direction of the pursuit signal, one might have expected a step function in the psychophysical task. That is, when the pursuit signal is in a particular direction, perception would be completely unambiguous, and the proportion of responses (as illustrated in Fig. 10) would have been at either 1.0 or 0.0, carrying over the results of conditions 2 and 6 until the transition point was met. Then, one might have expected a steep transition between the two perceptual states where the TVOR generated the necessary eye movements and the pursuit signal would be zero. Instead, the smooth transition between perceptual outcomes suggests that the magnitude of the pursuit signal plays a role as well, with small pursuit signals being less effect than larger pursuit signals. Previous work (Nawrot, 2003b) has shown that the magnitude of the pursuit signal has a very close relation to magnitude of perceived depth from motion parallax. That study showed that the change in magnitude of the pursuit signal over viewing distance is at the same rate as the change in perceived depth from motion parallax over viewing distance. However, it is not yet clear exactly how the visual system uses the pursuit signal to scale depth from motion parallax.

5. Discussion

We are still in the early stages of understanding the neural mechanisms responsible for the perception of depth from motion parallax. Obviously, the first stage relies on the perception of retinal motion. Beyond this motion perception stage, the motion parallax information must differentially activate neural units selective to opposing depth signs. While previous research has linked the perception of depth in motion parallax to the direction and speed of head translation, this is apparently not a representation of the parameters that are important for the neural mechanisms serving motion parallax. Head translation is important in so far as it creates the retinal stimulus for motion parallax in natural viewing conditions. Without the observer translation—active head translation or passive translation as in a vehicle—there would be no parallax stimulus created on the observer's retina. However, studying the parameter space of head translation does not inform us about the underlying visual processing mechanisms. The set of experiments presented here demonstrates that the visual system relies on the direction of the visually driven pursuit signal to determine the appropriate depth sign of the otherwise ambiguous retinal motion information.

The pursuit theory (Fig. 2) suggests a plausible neural mechanism to perform this depth sign disambiguation through facilitatory connections from the pursuit system. The model describes a relationship between pursuit direction and perceived depth sign in motion parallax that is fixed and lawful. An object whose image moves on the retina in the same direction as a concurrent pursuit eye movement is perceived nearer than the object serving as the pursuit target. This same rule applies regardless of the whether the observer translates actively, passively, or remains stationary and the stimulus moves. This fixed and lawful perceptual relationship suggests that the underlying neural mechanisms are a stable set of connections. With addition of the connections proposed to account for the spontaneous perceptual reversals in the kinetic depth effect (Nawrot & Blake, 1991), this simple neural network model may eventually account for a broad range of depth-from-motion phenomena.

Finally, while these results demonstrate that an extra-retinal pursuit signal serves an important function in the perception of depth from motion parallax, this does not mean that other cues have no role in the disambiguation of depth from motion parallax. Other visual cues may indeed play a role, but many previous studies of these cues may have to be reinterpreted because those studies failed to employ any eye-movement control or monitory.

Acknowledgments

This research was supported by NIH NEI R01-EY12541. The authors thank Chad Stockert for assistance in data collection, Frederick Miles and Elizabeth Nawrot for comments on the manuscript.

References

Abadi, R. V., Howard, I. P., Ohmi, M., & Lee, E. E. (2005). The effect of central and peripheral field stimulation on the rise time and gain of human optokinetic nystagmus. *Perception, 34*, 1013–1022.

Angelaki, D. E. (2004). Eyes on target: what neurons must do for the vestibuloocular reflex during linear motion. *Journal of Neurophysiology, 92*, 20–35.

Bradley, D. C., Chang, G. C., & Andersen, R. A. (1998). Encoding of three-dimensional structure-from-motion by primate area MT neurons. *Nature, 392*, 714–717.

Bradley, D. C., Qian, N., & Anderson, R. A. (1995). Integration of motion and stereopsis in middle temporal cortical area of macaques. *Nature, 373*, 609–611.

Braunstein, M. L., & Andersen, G. J. (1981). Velocity gradients and relative depth perception. *Perception & Psychophysics, 29*(2), 145–155.

Braunstein, M. L., & Tittle, J. S. (1988). The observer-relative velocity field as the basis for effective motion parallax. *Journal of Experimental Psychological Human Perceptual Performance, 14*, 582–590.

Bussettini, C., Miles, F. A., Schwarz, U., & Carl, J. R. (1994). Human ocular responses to translation of the observer and of the scene: dependence on viewing distance. *Experimental Brain Research, 79*, 484–494.

Cheng, M., & Outerbridge, J. S. (1975). Optokinetic nystagmus during selective retinal stimulation. *Experimental Brain Research, 23*, 129–139.

Demer, J. L., & von Noorden, G. K. (1988). Optokinetic asymmetry in esotropia. *Journal of Pediatric Ophthalmology and Strabismus, 25*, 286–292.

Epstein, W., & Park, J. (1964). Examination of Gibson's psychophysical hypothesis. *Psychological Bulletin, 62*, 180–196.

Farber, J. M., & McConkie, A. B. (1979). Optical motions as information for unsigned depth. *Journal of Experimental Psychology: Human Perception and Performance, 5*, 494–500.

Frankl, M., & Nawrot, M. (2005). Extra-retinal signals in motion parallax: support from eye movement asymmetries in strabismus. *Journal of Vision, 5*(8), 991a Abstract.

Gibson, J. J. (1950). *The perception of the visual world*. Boston: Houghton Mifflin Co.

Gibson, E. J., Gibson, J. J., Smith, O. W., & Flock, H. (1959). Motion parallax as a determinant of perceived depth. *Journal of Experimental Psychology, 58*, 40–51.

Gogel, W. C., & Tietz, J. D. (1977). Eye fixation and attention as modifiers of perceived distance. *Perceptual Motor Skills, 45*, 343–362.

Helmholtz, H. von (1909). In Southall, J.P.C. Treatise on physiological optics, 3rd. New York: Dover (1962).

Hershberger, W. A., & Starzec, J. J. (1974). Motion-parallax cues in one-dimensional polar and parallel projections: differential velocity and acceleration/displacement chance. *Journal of Experimental Psychology, 103*, 717–723.

Howard, I. P., & Ohmi, M. (1984). The efficiency of the central and peripheral retina in driving human optokinetic nystagmus. *Vision Research, 24*, 969–976.

Kawano, K. (1999). Ocular tracking: behavior and neurophysiology. *Current Opinion in Neurobiology, 9*, 467–473.

Kitazaki, M., & Shimojo, S. (1998). Surface discontinuity is critical in a moving observer's perception of object's depth order and relative motion from retinal image motion. *Perception, 27*, 1153–1176.

Koenderink, J. J. (1986). Optic flow. *Vision Research, 26*, 161–180.

Komatsu, H., & Wurtz, R. H. (1988a). Relation of cortical areas MT and MST to pursuit eye movements. III. Interaction with full-field visual stimulation. *Journal of Neurophysiology, 60*, 621–644.

Komatsu, H., & Wurtz, R. H. (1988b). Relation of cortical areas MT and MST to pursuit eye movements. I. Localization and visual properties of neurons. *Journal of Neurophysiology, 60*, 580–603.

Krauzlis, R. J. (2004). Recasting the smooth pursuit eye movement system. *Journal of Neurophysiology, 91*, 591–603.

Miles, F. A. (1993). The sensing of rotational and translational optic flow by the primate optokinetic system. In F. A. Miles & J. Wallamn (Eds.), *Visual motion and its role in the stabilization of gaze* (pp. 393–403). New York: Elsevier.

Miles, F. A. (1998). The neural processing of 3-D visual information: evidence from eye movements. *European Journal of Neuroscience, 10*, 811–822.

Miles, F. A., & Busettini, C. (1992). Ocular compensation for self-motion: visual mechanisms. *Annual Review of the New York Academy of Science, 656*, 220–232.

Miles, F. A., Kawano, K., & Optican, L. M. (1986). Short-latency ocular following responses of monkey. I. Dependence on temporo-spatial properties of the visual input. *Journal of Neurophysiology, 56*, 1321–1354.

Morris, E. J., & Lisberger, S. G. (1987). Different responses to small visual errors during initiation and maintenance of smooth-pursuit eye movements in monkeys. *Journal of Neurophysiology, 58*, 1351–1369.

Nadler, J.W., Angelaki, D.E., DeAngelis, G.C. (2005). MT neurons combine visual motion with extra-retinal signals to code depth sign from motion parallax. Society for Neuroscience Abstracts, 583.5.

Naji, J. J., & Freeman, T. C. A. (2004). Perceiving depth order during pursuit eye movement. *Vision Research, 44*, 3025–3034.

Nawrot, M. (2003a). Eye movements provide the extra-retinal signal required for the perception of depth from motion parallax. *Vision Research, 43*, 1553–1562.

Nawrot, M. (2003b). Depth from motion parallax scales with eye movement gain. *Journal of Vision, 3*, 841–851.

Nawrot, M., & Blake, R. (1991). A neural network model of kinetic depth. *Visual Neuroscience, 6*, 219–227.

Nawrot, M., Frankl, M., & Stockert, C. (2004). Elevated motion parallax thresholds are related to eye movement anomalies in strabismus. *Journal of Vision, 4*(8), 202a Abstract 202.

Nawrot, M., Nordenstrom, B., & Olson, A. (2004). Disruption of eye movements by ethanol intoxication affects perception of depth from motion parallax. *Psychological Science, 15*, 858–865.

Nawrot, M., & Stockert, C. (2005). Motion parallax in movies: background motion, eye movement signals, and depth. *Journal of Vision, 5*, 644a.

Newsome, W. T., Wurtz, R. H., & Komatsu, H. (1988). Relation of cortical areas MT and MST to pursuit eye movements. II. Differentiation of retinal from extra-retinal inputs. *Journal of Neurophysiology, 60*, 604–620.

Ono, H., & Steinbach, M. J. (1990). Monocular stereopsis with and without head movement. *Perception & Psychophysics, 48*, 179–187.

Ono, H., & Ujike, H. (1994). Apparent depth with motion aftereffect and head movement. *Perception, 23*, 1241–1248.

Ono, H., & Ujike, H. (2001). Depth thresholds of motion parallax as a function of head movement velocity. *Vision Research, 41*, 2835–2843.

Ono, H., & Ujike, H. (2005). Motion parallax driven by head movement: conditions for visual stability, perceived depth, and perceived concomitant motion. *Perception, 34*, 477–490.

Ono, H., & Wade, N. J. (2005). Depth and motion in historical descriptions of motion parallax. *Perception, 34*, 1263–1273.

Post, R. B., & Leibowitz, H. W. (1985). A revised analysis of the role of efference in motion perception. *Perception, 14*, 631–643.

Rogers, B., & Graham, M. (1979). Motion parallax as an independent cue for depth perception. *Perception, 8*, 125–134.

Rogers, S., & Rogers, B. J. (1992). Visual and nonvisual information disambiguate surfaces specified by motion parallax. *Perception & Psychophysics, 52*, 446–452.

Roy, J. P., Komatsu, H., & Wurtz, R. H. (1992). Disparity sensitivity of neurons in monkey extrastriate area MST. *Journal of Neuroscience, 12*, 2478–2492.

Schweigart, G., Maurer, C., & Mergner, T. (2003). Combined action of smooth pursuit eye movements, optokinetic reflex, and vestibulo-ocular reflex in macaque monkey during transient stimulation. *Neuroscience Letters, 340*, 217–220.

Sumnall, J. H., Freeman, T. C., & Snowden, R. J. (2003). Optokinetic potential and the perception of head-centred speed. *Vision Research, 43*, 1709–1718.

Teuber, H. (1960). In H. W. Magoun (Ed.), *Section I, Neurophysiology* (Vol. II). *Perception. Handbook of physiology* (pp. 1595–1668). Baltimore: Waverly Press.

Thompson, A. M., & Nawrot, M. (1999). Abnormal depth perception from motion parallax in amblyopic observers. *Vision Research, 39*, 1407–1413.

Ujike, H., & Ono, H. (2001). Depth thresholds of motion parallax as a function of head movement velocity. *Vision Research, 41*, 2835–2843.

Upadhyay, U. D., Page, W. K., & Duffy, C. J. (2000). MST responses to pursuit across optic flow with motion parallax. *Journal of Neurophysiology, 84*, 818–826.

Wade, N. J. (1998). *A natural history of vision*. London: Cambridge: MIT Press.

Westall, C. A., Eizenman, M., Kraft, S. P., Panton, C. M., Chatterjee, S., & Sigesmund, D. (1998). Cortical binocularity and monocular optokinetic asymmetry in early-onset esotropia. *Investigative Ophthalmology and Visual Science, 39*, 1352–1360.

Wetherill, G. B., & Levitt, H. (1965). Sequential estimation of points on a psychometric function. *The British Journal of Mathematical and Statistical Psychology, 18*, 1–10.

Wheatstone, C. (1839). Contributions to the physiology of vision-Part the first. On some remarkable, and hitherto unobserved, phenomena of binocular vision. *Philosophical Transactions of the Royal Society, 142*, 1–17.