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Additivity of retinal and pursuit velocity in the perceptions of depth and rigidity from object-produced motion parallax

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Abstract. Two psychophysical experiments were conducted to investigate the mechanism that generates stable depth structure from retinal motion combined with extraretinal signals from pursuit eye movements. Stimuli consisted of random dots that moved horizontally in one direction (ie stimuli had common motion on the retina), but at different speeds between adjacent rows. The stimuli were presented with different speeds of pursuit eye movements whose direction was opposite to that of the common retinal motion. Experiment 1 showed that the rows moving faster on the retina appeared closer when viewed without eye movements; however, they appeared farther when pursuit speed exceeded the speed of common retinal motion. The 'transition' speed of the pursuit eye movement was slightly, but consistently, larger than the speed of common retinal motion. Experiment 2 showed that parallax thresholds for perceiving relative motion between adjacent rows were minimum at the transition speed found in experiment 1. These results suggest that the visual system calculates head-centric velocity, by adding retinal velocity and pursuit velocity, to obtain a stable depth structure.

1 Introduction

A fundamental goal of vision is to determine the depth structure of visual scenes. One important source of information for this structure is motion parallax (eg Ono et al 1986; Rogers and Graham 1979). Vivid and stable depth is seen when a horizontal shearing motion is presented (a) on a stationary monitor and yoked to lateral head movements, or (b) on a horizontally translating monitor and yoked to the monitor movement. In both cases, the portion that moves in the same direction as that of the object translation relative to the head appears in front of another portion that moves in the opposite direction. Perceived relative motion is suppressed when stable depth is seen; this suppression suggests that the visual system directly converts retinal motion into depth (Ono and Steinbach 1990; Ono and Ujike 2005; Sakurai and Ono 2000).

Perceived depth order is unstable when retinal shearing motion is not yoked to head or monitor movement,(1) just as it is with the kinetic depth effect. This suggests that stable depth order requires retinal motion to be combined with extraretinal signals (eg Nawrot 2003a, 2003b; Ono et al 1986). Nawrot recently proposed that critical extraretinal signals originate from pursuit eye movements. Pursuit eye movements are triggered not only by pursuing a translating object but also by fixating a stationary stimulus during head translation. He thus claimed that pursuit signals are available with either head or object movement and determine the perceived depth order.

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(1) Note that additional retinal cues are also known to disambiguate the depth order of moving patterns, such as perspective (Braunstein and Andersen 1981; Rogers and Rogers 1992), partial occlusion (Fang and He 2004), and visual friction (Gilroy and Blake 2004).

A simple but important situation where Nawrot's model cannot predict depth order is that in which a retinal stimulus contains common motion (ie translational component) in addition to shearing motion.

For a stimulus seen through a window, with shearing-motion and common-motion components, the portion that moves faster on the retina appears closer without eye movement (Braunstein and Andersen 1981). On the basis of this idea, one could formulate an extreme version of a retinal model, which postulates that retinal velocity is the sole determinant of the depth order. This model differs from Nawrot's model in that the retinal model assumes that extra-retinal pursuit velocity is not necessary for determining depth order. Braunstein and Tittle (1988) tested this possibility experimentally, but their results are not conclusive because the authors did not control for eye movements.

In this paper we propose that a single framework predicts perceived depth order irrespective of the presence of common retinal motion or pursuit eye movements. In this additive model, the visual system adds the pursuit velocity and the retinal velocity of each portion of the moving structure. Then, the visual system compares the resulting 'head-centric' velocities among different portions of the visual field and assigns a closer distance to the portion that has a larger head-centric velocity. The additive model is represented by the following inequalities:

$$\begin{aligned} &\text{if } |v_1 + v_{\text{pursuit}}| \geqslant |v_2 + v_{\text{pursuit}}|,\ D_1 \leqslant D_2\,, \\ &\text{otherwise, } D_1 > D_2\,. \end{aligned} \tag{1}$$

Here D_1 and D_2 are the perceived distances of moving elements in which the angular velocities of retinal motion are v_1 and v_2, respectively, and v_{pursuit} denotes the angular velocity of pursuit eye movements.(2) The calculated value in inequality (1), $v_i + v_{\text{pursuit}}$, for the ith portion is equal to the head-centric velocity field (Braunstein and Tittle 1988; Naji and Freeman 2004). Given that the unstable perceived depth order is statistically represented by $D_1 = D_2$ (sometimes $D_1 > D_2$ and at other times $D_1 < D_2$), the additive model predicts that perceived depth order is unstable when $(v_1 + v_2)/2 + v_{\text{pursuit}} = 0$. In this condition, sensitivity to relative motion is expected to be maximal, because there is no stable depth perception to suppress the perception of relative motion (eg Ono and Steinbach 1990). Note that this model differs from the retinal model because the portion that moves faster on the retina is not always predicted to appear closer (eg $D_1 > D_2$ when $|v_1| > |v_2|$, given $-v_{\text{pursuit}} < (v_1 + v_2)/2 < 0$, $v_{\text{pursuit}} > 0$, and $v_1, v_2 < 0$).

To examine whether the additive model is viable, we experimentally introduced different extents of 'common' motion on the retina (ie $v_1 + v_2 \neq 0$), and different velocities of pursuit eye movements. Specifically, we chose the values of v_1 and v_2 so that (a) they had the same motion direction relative to a pursuit point at any moment, and (b) the absolute value of common motion [ie the translational component, $(v_1 + v_2)/2$] was larger than that of relative motion [ie the shearing component, $(v_1 - v_2)/2$]. The direction of common retinal motion was kept opposite to that of the pursuit eye movements. Under such conditions, the two models give different predictions for both perceived depth order and perceived relative motion. Therefore, for a given stimulus condition, we measured the consistency of perceived depth order (experiment 1) and the threshold for perceived relative motion (experiment 2).

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(2) The velocities can be interpreted as referring to perceived velocities rather than physical velocities. See section 4 and figure 5 for the estimates obtained from experiments 1 and 2.

2 Experiment 1

We manipulated the speeds of common retinal motion and pursuit eye movements independently, and measured perceived depth order between the rows defined by the speed differences of random dots (figure 1). More specifically, we measured the frequency for which the rows moving faster on the retina appear closer than the rows moving slower. We tested the two models discussed in the introduction. The prediction from the additive model is shown in figure 2a. Based on inequality (1), the additive model predicts that the rows moving faster on the retina will appear *farther* when the speed of pursuit exceeds that of common retinal motion, resulting in three different 'transition' speeds of pursuit [ie $v_{\text{pursuit}} = -(v_1 + v_2)/2$]. The retinal model predicts that the rows moving faster on the retina always appear closer (figure 2b).

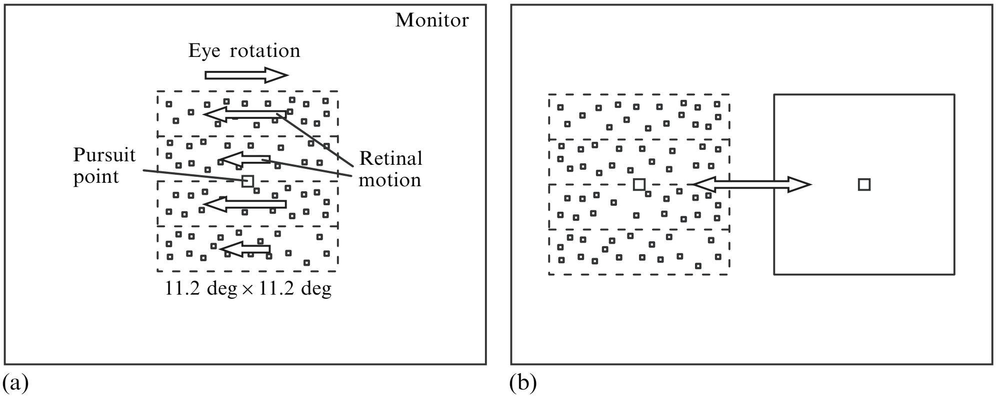

Figure 1. A schematic representation of the stimuli used in this study. (a) The four arrows superimposed on the random dots represent dot motion (ie retinal velocity); the arrow drawn above the dot regions represents pursuit eye movements (ie pursuit velocity). The direction of retinal velocity was always opposite to that of pursuit eye movements. (b) The stimulus region and the pursuit point moved horizontally.

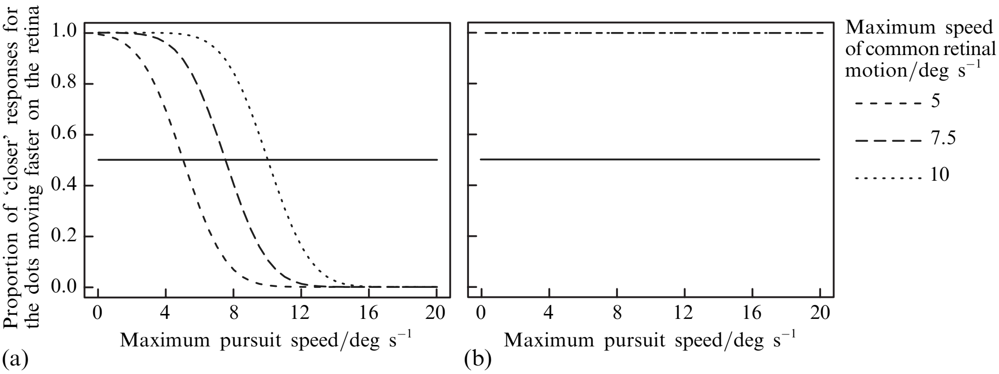

Figure 2. Predictions for the depth-order judgment (experiment 1) based on the additive and retinal models [(a) and (b), respectively]. Dashed lines represent the predictions; horizontal solid lines represent 'ambiguous' percepts.

2.1 *Methods*

2.1.1 *Observers.* Six observers participated in the experiment. All observers were naive to the purpose of the experiment, except for one of the authors (HM). All had normal or corrected-to-normal vision.

2.1.2 *Apparatus and stimuli.* A personal computer (Apple Power Macintosh G3) was used to generate stimuli and to collect data. Stimuli were presented on a gamma-corrected

17-inch CRT monitor (Apple Multiple Scan 720 Display), subtending 33.8 deg × 26.7 deg of visual angle. Stimulus presentation was synchronised with the monitor's vertical refresh rate (75 Hz).

The stimuli consisted of 300 bright dots randomly distributed within an imaginary square-shaped region (11.2 deg × 11.2 deg of visual angle—figure 1a). Each dot subtended 4.5 min of arc × 4.5 min of arc of visual angle, and the sub-pixel position was represented by the anti-alias method. A pursuit point (22.5 min of arc × 22.5 min of arc) was presented at the centre of the stimulus region. The luminance of the dots and the pursuit point was 30.52 cd m^{-2}, and that of the background was 0.02 cd m^{-2}.

The random dots and the pursuit point moved horizontally and sinusoidally on the monitor (figure 1b) as follows: the horizontal shift of the pursuit point x_{pursuit} on the monitor was calculated by

$$x_{\mathrm{pursuit}} = a \sin(2\pi\tau/P) \,, \tag{2}$$

where a is the amplitude of eye rotation, τ denotes time ($0 < \tau < 4.8$ s), and P is the period (2.4 s). The value of a was chosen from 0, 1.5, 3.0, 4.5, 6.0, and 7.5 deg for each trial. These values of a produced maximum pursuit speeds of 0, 4, 8, 12, 16, and 20 deg s^{-1}, respectively. The horizontal displacement x_{dot} of each random dot on the monitor was calculated by

$$x_{\mathrm{dot}} = \begin{cases} [a - b(1+d)]\sin(2\pi\tau/P) & \text{for the dots moving fast on the retina}\,, \\ [a - b(1-d)]\sin(2\pi\tau/P) & \text{for the dots moving slowly on the retina}\,, \end{cases} \tag{3}$$

where b is the amplitude of the common motion on the retina and d is the parallax amplitude. The value of b was chosen from 1.9, 2.8, and 3.7 deg of visual angle for each trial. These values of b produced maximum common-motion speeds of 5, 7.5, and 10 deg s^{-1}, respectively. The value of d was constant, 0.07.

The stimulus region was divided into four equally spaced rows. If the dots moving faster on the retina were presented in the first and the third rows of the stimulus region for a trial, the other dots were presented in the second and the fourth rows, or vice versa. The parallax amplitude resulted in 61 min of arc of equivalent disparity between the dots moving faster on the retina and the other dots (assumed interocular distance: 6.5 cm).

The stimulus region was kept square by redrawing the random dots on one side if they moved beyond the other side. This procedure ensured that the observers received the same retinal stimulation across the six pursuit velocities for each common retinal motion, when the observers tracked the pursuit point accurately. We also checked the accuracy of the pursuit eye movements (see sections 2.1.4 and 2.2.1).

Note that the assumption for this experiment was that the observers used extraretinal velocity signals from pursuit eye movement, not retinal cues, to process the velocity of eye rotation. One could argue that the information regarding pursuit velocity was available from a retinal cue, namely, the trapezoidal transformation of the stimulus area (Rogers and Rogers 1992). However, in this experiment, this perspective transformation was not an effective cue for processing the pursuit velocity, because (a) the density of random dots was low and the stimulus region did not have a sharp boundary, and (b) the dots had a common-motion component and the boundary (or overall shape) of the stimulus was difficult to detect.

2.1.3 *Procedure.* Observers viewed the stimuli with their right eye. Their left eye was covered with an eye patch. The viewing distance was 47 cm, relatively shorter than that of standard psychophysical experiments, selected so that the stimulus moved over a wider visual angle on the 17-inch monitor. Each observer's head was stabilised with a chin-and-forehead-rest. The experiment was conducted in a darkened room, and the objects outside the monitor were dark, so that no stationary reference was presented.

At the beginning of each trial, only the pursuit point was presented for 1.2 s (half a cycle). The random dots without relative motion (ie $d = 0$) were added and presented for 1.2 s; finally the dots were presented with relative motion (ie the value of d changed to 0.07) and presented for 4.8 s (two cycles). The aim of presenting the dots without relative motion was to avoid a depth judgment with possible inaccurate eye movements triggered by the onset of moving dots (Mestre and Masson 1997). During this sequence observers were required to maintain fixation on the pursuit point as accurately as possible. After each observation sequence, observers were required to report which rows appeared in front of the other rows using a two-alternative forced choice (ie the first and third rows appeared in front of the second and fourth ones, and vice versa). Observers responded by pressing the 'upward arrow' or 'downward arrow' key (the first and third rows in front or the second and fourth rows in front, respectively) on the keyboard. Observers were not required to make speedy judgments. The inter-trial interval was 1.5 s.

Each observer completed 396 trials, which were divided into eleven blocks. Each block comprised 36 trials (6 pursuit speeds × 3 common-motion speeds × 2 phases of motion-defined grating). The order of presentation was randomised within each block. The initial direction of movement (ie left or right) of the pursuit point was randomly selected for each trial). The first block constituted practice trials. The first six blocks and the last five blocks were conducted on different days.

2.1.4 *Eye-movement recording.* For two observers, in separate sessions, we measured eye movements during stimulus observations with a video eye-tracker (El-Mar Vision2000; sampling rate, 120 Hz). Their eye-position data were recorded for one block (36 trials) in which the procedure was identical to that of the depth-order judgment task. With the exception of the no-eye-movement conditions, the horizontal component of the eye-movement data for each trial was used to calculate pursuit velocity. Specifically, after smoothing the position data (the moving average of five frames), pursuit velocity was calculated from the position data and fitted with a cosine curve for the last two cycles (ie 4.8 s of stimulus presentation). We calculated the three best-fitting parameters(3)—amplitude of the cosine curve, phase of the cosine curve, and a direct current (a vertical shift of the cosine curve)—with a least-squares method. The amplitude of the cosine curve was used to estimate the maximum pursuit velocity for each condition.

2.2 *Results and discussion*

2.2.1 *Eye-movement recording.* Figure 3 shows the 'measured' maximum pursuit velocity as a function of 'simulated' pursuit velocity for each of the three common retinal motions. The results clearly showed that the data for the three common retinal motions were close to the solid line, representing the expected velocities, and that there were no differences among them. The dotted lines represent the situations where the random dots and not the pursuit point are followed. An F test was performed to find out whether or not common retinal motion influences pursuit velocity. For each observer, there was no significant error reduction by assuming three different regression lines for the three common motions ($F_{4,9} = 0.23$, $p > 0.9$; $F_{4,9} = 1.37$, $p > 0.3$). Therefore, we concluded that observers were able to maintain tracking of the pursuit point accurately, irrespective of the different common motions on the retina, and proceeded with the analyses of the data on the perceived depth order.

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(3) We were not able to calculate the pursuit lag because the temporal reference of the tracking eye movement with respect to the motion of the stimulus was not available. As suggested by Naji and Freeman (2004), we assumed that neither the delay in pursuing the moving stimuli nor the resulting 'common motion' would influence the depth judgments.

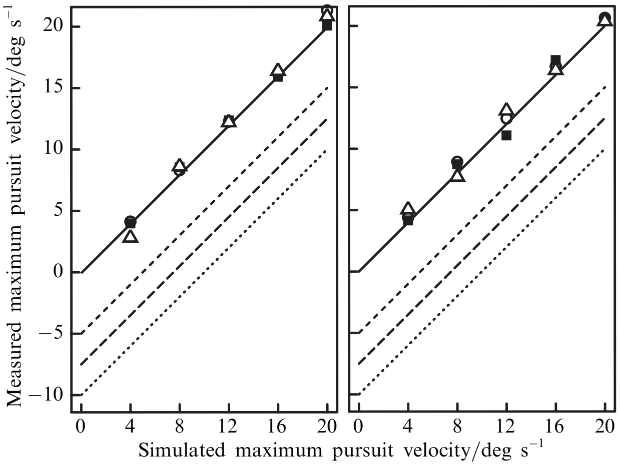

Figure 3. Results of eye-movement recording ($n = 2$; the plot on the right shows the results of author HM). Solid lines represent the perfect tracking of the pursuit point; dashed lines represent the case where the eye completely tracks one of the random dots (at the mean speed of the dots).

2.2.2 *Depth order.* For each condition, we computed the proportion of 'closer' responses for the rows moving faster on the retina. For each observer, a cumulative Gaussian function was fitted to the proportions for each of the three common retinal motions by a maximum-likelihood method. Figure 4 shows the means across the six observers as a function of maximum pursuit speed together with the best-fitting lines for the pooled data. The lines were qualitatively consistent with the means of the best-fitting data from individual observers. The maximum pursuit speeds where the proportion of closer responses was 0.5 (transition pursuit speed) were subject to one-way repeated-measures ANOVA with the factor of maximum common-motion speed (5, 7.5, 10 deg s^{-1}). The main effect was significant ($F_{2,10} = 42.525$, $p < 0.0001$). Multiple comparisons (Ryan's method) revealed that all three speeds were significantly different from each other (the mean values are shown in figure 5). These results support the additive model: the visual system calculates the object velocity relative to the head, by adding retinal-image and pursuit velocities, and then uses it to determine the depth order of moving patterns. In contrast, Nawrot's model does not predict depth order for our stimulus, because his model does not take into account the common retinal motion.

The additive model we propose explains the results of Braunstein et al (Braunstein and Andersen 1981; Braunstein and Tittle 1988) when there is no eye movement. That is, depth order is predicted by assuming that the information about the head-centric common motion is available from common retinal motion. (Regardless of the movement of the 'stimulus window' on the monitor, their stimuli can be partitioned into two

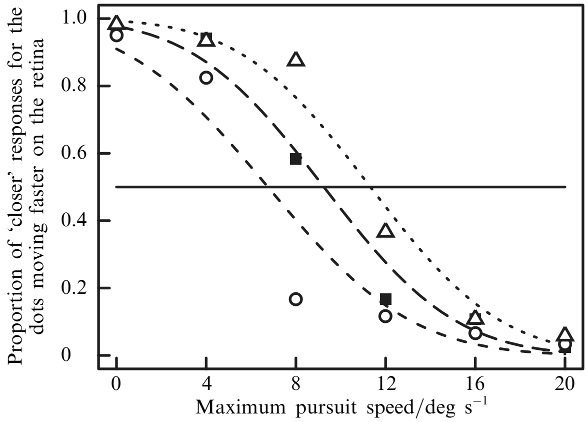

Figure 4. Results of experiment 1 (depth-order judgment, $n = 6$). Dashed lines represent fitted cumulative Gaussian functions; horizontal solid line represents 'ambiguous' percepts.

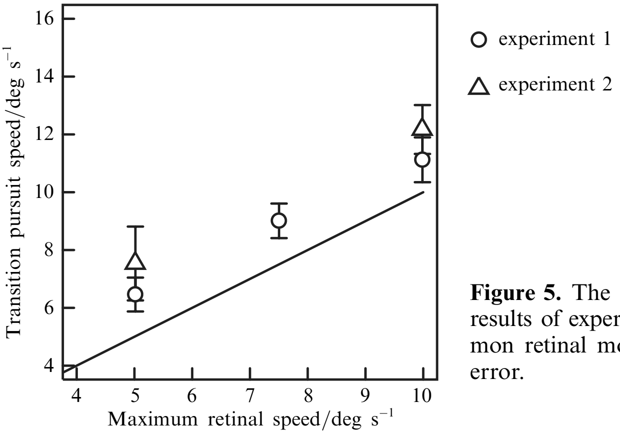

Figure 5. The transition speed calculated with the results of experiments 1 and 2 as a function of common retinal motion. Error bars represent standard error.

components—common and shearing motions.) It is also true that the additive model (and Nawrot's model) can explain Braunstein et al's results, provided that the common retinal motion of the moving elements is cancelled completely by the pursuit eye movements (only shearing retinal motion is present in this case). Apart from the control of eye movements, the difference between Braunstein et al's stimulus and ours is the type of shearing motion—a vertical gradient in Braunstein et al's case, a square-wave profile in our case.

As noted in the introduction, Ono and Steinbach (1990) and Ono and Ujike (2005) reported that perceived relative motion is suppressed when stable depth is observed. Thus, if we measure and compare the sensitivities to perceived relative motion with different extents of common retinal motion and pursuit velocity, we can obtain additional evidence to support the additive model. We examined the additive model further in experiment 2.

3 Experiment 2

We measured parallax thresholds for perceiving relative motion using the same stimuli as in experiment 1. The independent variables were also the same, with the exception that we used only two of the three common retinal motions—maximum speeds of 5 and 10 deg s^{-1}. To simplify the judgment of the relative motion between the rows, we embedded two vertical (probe) lines in the second and the third rows of the stimuli. Each observer's task was to adjust the extent of relative motion between the probe lines until the extent of relative motion reached the threshold for detection (d in equation 3).

As noted in the introduction, sensitivity to perceived relative motion was expected to be maximal when the depth order was ambiguous (ie $D_1 > D_2$ or $D_1 < D_2$, but statistically $D_1 = D_2$). If the additive model was correct, sensitivity to relative motion was expected to be maximal when the pursuit speed was the same as the retinal common-motion speed (opposite in direction). More specifically, the additive model predicted that the parallax thresholds for relative motion were minimal at the transition pursuit speeds found in experiment 1. The retinal model did not predict such results.

3.1 *Methods*

3.1.1 *Observers.* Eight observers participated in the experiment. All observers were naive to the purpose of the experiment, except one of the authors (HM). All had normal or corrected-to-normal vision. Two of them had participated in experiment 1.

3.1.2 *Apparatus and stimuli.* The apparatus and the stimuli were the same as those used in experiment 1, except for the following: two vertical lines (each line, 4.5 min of arc × 45.0 min of arc) were presented for 267 ms at the centre of the second and the third rows of the stimuli when they passed through the centre of the screen. Each line and the random-dot background moved together (ie each line had the same velocity as that of the background). The lines had the same luminance as the random dots, and the horizontal shift between the two lines was 0 when they passed through the exact centre of the screen.

3.1.3 *Procedure.* Each observer's task was to determine the lower parallax limit for the perceived relative motion between the two vertical lines. The observers adjusted the parallax amplitude (d in equation 3) of the lines and the random dots by pressing the 'upward arrow' or 'downward arrow' key (increasing or decreasing the parallax amplitude, respectively) on the keyboard. A similar technique was used in Ono and Ujike (2005) and Ujike and Ono (2001). The parallax amplitude of the random dots varied in accordance with that of the lines. The stimuli were presented until the observers were satisfied with their adjustment (maximum exposure duration, 120 s). The starting values of the parallax amplitude were set to 0 or 0.14 to counterbalance the effect of response biases. The other experimental settings were the same as those used in experiment 1.

Each observer completed 108 trials, which were divided into five blocks. The first block, composed of 12 trials, was for practice. Each of the four experimental blocks comprised 24 trials (6 pursuit speeds × 2 common-motion speeds × 2 starting parallaxes). The order of presentation was randomised in each block. The initial direction of movement of the pursuit point (left or right) and the assignments of the dot speeds to the four rows were randomly selected for each trial.

3.2 *Results and discussion*

Figure 6 shows the parallax thresholds for perceived relative motion averaged over the eight observers. A two-way repeated-measures ANOVA was performed on the parallax thresholds with the factors of maximum common-motion speed (5, 10 deg s^{-1}) and maximum pursuit speed (0, 4, 8, 12, 16, 20 deg s^{-1}). The interaction and the two main effects were significant ($F_{5,35} = 2.725$, $p < 0.05$ for interaction; $F_{1,7} = 34.51$, $p < 0.001$ for common motion; $F_{5,35} = 3.014$, $p < 0.05$ for pursuit).

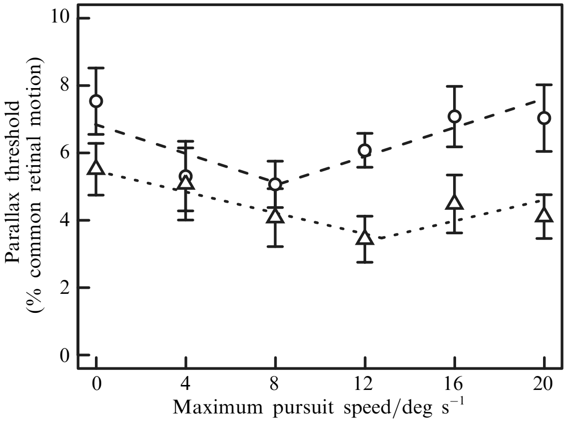

Figure 6. Results of experiment 2 (parallax thresholds for perceiving relative motion, $n = 8$). Dashed lines are the best-fitting curves. Error bars represent standard error.

To estimate and to compare the pursuit speeds in which the parallax threshold was minimal, a V-shaped curve was fitted to the data for each common retinal motion. More specifically, parallax threshold Ts for perceived relative motion were fitted with a symmetric V-shaped function defined by

$$T = \begin{cases} T_{\min} + s(v - v_{\min}), & v \geqslant v_{\min}\,, \\ T_{\min} - s(v - v_{\min}), & v < v_{\min}\,, \end{cases} \tag{4}$$

where s is the slope of the component line, v denotes the maximum pursuit speed, and $v_{\min}$ is the maximum pursuit speed that results in the 'lowest' threshold $T_{\min}$. The three free parameters, s, $v_{\min}$, and $T_{\min}$, were estimated with a least-squares method. The lines in figure 6 represent the best-fitting curves for the pooled data for the eight observers, and are qualitatively consistent with the data for individual observers. A paired t test (two-tailed) revealed a significant difference in $v_{\min}$ between the two common-motion speeds[4] ($t_5 = 2.96$, $p < 0.05$). All the obtained values of slope s were positive (mean, 0.64; SD, 0.37), indicating that the fitted curve had an 'upright' and not an 'inverted' V-shape. The mean values of $v_{\min}$ are shown in figure 5 ($n = 6$ and $n = 8$ for common-retinal-motion speeds of 5 and 10 deg s^{-1}, respectively), and were close to the transition speeds obtained in experiment 1. These results suggest that sensitivity to relative motion was maximal when pursuit and retinal common-motion velocities have opposite directions of movement but have a similar magnitude. These results are consistent with the additive model.

4 General discussion

The results from the two experiments provide evidence for the additive model, in which retinal and pursuit velocities are summed to obtain stable depth from motion parallax. We agree with Nawrot's claim that pursuit signals are important in recovering depth from motion parallax. The additive model we propose, however, is broader than Nawrot's 'heuristic' rule (Nawrot 2003b, page 1559), because it can predict perceived depth order even when the retinal motion contains a common-motion component.

Although our results generally support the additive model, they indicate that the visual system does not accurately process the head-centric velocity. Figure 5 shows the mean transition speed as a function of the common-motion speed on the retina. If the visual system accurately processed the head-centric velocity, the obtained data would be on the oblique line in figure 5. The results, however, reveal a constant difference invariant across the common retinal speeds. The difference is qualitatively consistent with the empirical finding that pursuit velocity tends to be 'underestimated' with respect to retinal velocity (the Filehne illusion, eg Freeman et al 2002). Despite the constant error, our results suggest that the visual system uses the perceived pursuit velocity to construct a head-centric representation, as argued by Freeman and Fowler (2000), and shows the importance of processing head-centric velocity in perceptual tasks as argued by Morvan and Wexler (2005).

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[4] Data of two observers were excluded from this test because we could not calculate $v_{\min}$ for their common-retinal-motion speed of 5 deg s^{-1}, as their data were too variable. We speculate that their high variability was due to difficulty in judging the slow relative motion. That is, the motion threshold was higher at the common-retinal-motion speed of 5 deg s^{-1} than at that of 10 deg s^{-1}, as shown in figure 6.

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