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Role of feedback in the accuracy of perceived direction of motion-in-depth and control of interceptive action

Rob Gray [a,*], D. Regan [b], Brooke Castaneda [a], Randy Sieffert [a,c]

[a] *Department of Applied Psychology, Arizona State University, 7001 E. Williams Field Rd., Mesa, AZ 85212, USA*
[b] *Department of Psychology, York University, Toronto, Canada*
[c] *Intel Corporation, USA*

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Abstract

We quantified the accuracy of the perception of the absolute direction of motion-in-depth (MID) of a simulated approaching object using a perceptual task and compared those data with the accuracy of estimating the passing distance measured by means of a simulated catching task. For the simulated catching task, movements of the index finger and thumb of the observer's hand were tracked as participants tried to "catch" the simulated approaching object. A sensation of MID was created by providing monocular and/or binocular retinal image information. Visual stimuli were identical for perceptual and simulated catching tasks. We confirm previous reports that in the perceptual task, observers judged the object to pass wider of the head than indicated by the visual information provided. Although accuracy improved when auditory feedback was added to the perceptual (button pressing) task, consistent overestimates were still recorded. For the no-feedback simulated catching task, observers consistently overreached, i.e., the hand was further away from the midline than the simulated object at the time of hand closure. When auditory feedback was added to the simulated catching task successful catching was achieved. The relative accuracy in binocular and monocular conditions for individual observers could be partially explained by individual differences in sensitivity to unidirectional changes in angular size and changes in relative disparity. We conclude that catching an approaching ball requires that errors in the perceived direction of MID are corrected by feedback-driven learning in the motor system, and that this learning is more easily achieved for the catching action than for button pressing.

Keywords: Motion-in-depth; Binocular vision; Action; Interception

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1. Introduction

It has been proposed that a person intercepts an approaching object, for example, when hitting or catching a ball, by continually monitoring visual information about *where* the object will be at some future instant and *when* it will be there. What visual information is used to judge *when* an approaching object will arrive (the time to collision) is a question that has been studied extensively (see Hecht & Savelsbergh, 2004; Regan & Gray, 2000 for recent reviews). On the other hand, the judgment of *where* an approaching object will be when it reaches the observer has received considerably less attention by researchers (Williams, Davids, & Williams, 1999). In particular, it is not clear from previous research which sources of visual information are used for judgments of the absolute direction of motion-in-depth (MID) of an approaching object and how this information is used to control motor action.

Either monocular or binocular visual information correlate with the angular direction of MID of an object approaching at a constant velocity relative to the body

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[*] Corresponding author. Tel.: +1 480 727 1340; fax: +1 480 727 1538.
E-mail address: robgray@asu.edu (R. Gray).

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midline and also with the lateral distance at which the object will cross the vertical plane that contains the eyes (the *passing distance*).

First, consider monocular information. With reference to Fig. 1A, the direction of MID (β) is given by

$$\beta = \tan^{-1}\frac{2R\dot{\alpha}}{D\dot{\theta}}, \qquad (1)$$

where $\dot{\alpha}$ is angular lateral speed of the object, $\dot{\theta}$ is the rate of change of the object's angular subtense, D is the distance of the object from the eye and R is the object's radius. The passing distance (X_{p}) is given by

$$X_{\mathrm{p}} \approx \frac{2R\dot{\alpha}}{\dot{\theta}}. \qquad (2)$$

(Bootsma, 1991; Regan & Kaushal, 1994). Eqs. (1) and (2) are available to either eye alone.[1]

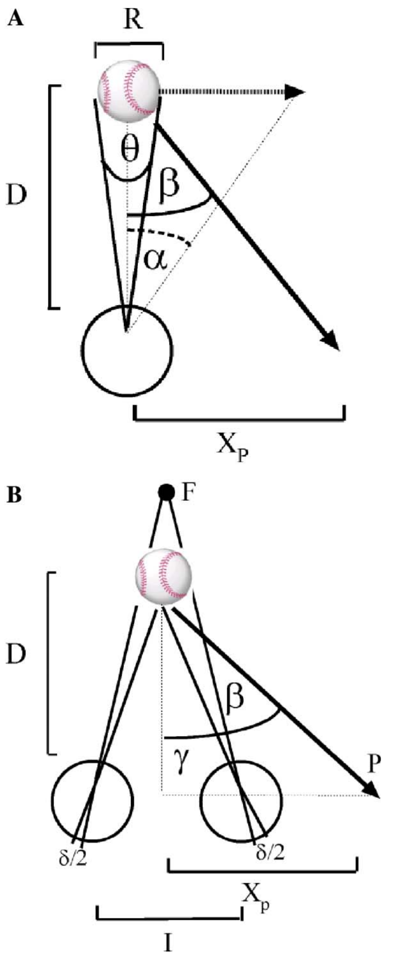

Fig. 1. Visual information about the direction of motion-in-depth (MID) of an approaching object. β is the angular direction of MID relative to the midline. X_{p} is the passing distance. (A) Monocular information about the direction of MID. A ball radius R travels at a constant speed along a straight line (shown by the heavy arrow). Its instantaneous distance from the observer's is eye (open circle) is D. θ is the ball's instantaneous angular subtense and α is the angular change in its lateral position (i.e., along the axis shown with the dotted arrow). (B) Binocular information about the direction of MID. A ball travels at a constant speed on a straight line (shown by the heavy arrow) some distance from the observer's eyes (open circles). δ is the retinal disparity of the ball relative to a fixed reference point (F) and I is the interpupillary separation. α is the angular change in its lateral position (i.e., along the axis shown with the dotted arrow). See text for details.

Fig. 1B illustrates binocular correlates of the direction of MID and passing distance. For motion within the horizontal meridian the direction of MID is given by

$$\beta = \tan^{-1}\left\{\frac{I[\dot{\varepsilon}_{\mathrm{R}}/\dot{\varepsilon}_{\mathrm{L}}]+1}{2D[\dot{\varepsilon}_{\mathrm{R}}/\dot{\varepsilon}_{\mathrm{L}}]-1}\right\}, \qquad (3)$$

$$X_{\mathrm{p}} = I\left\{\frac{I[\dot{\varepsilon}_{\mathrm{R}}/\dot{\varepsilon}_{\mathrm{L}}]+1}{\dot{\varepsilon}_{\mathrm{R}}/\dot{\varepsilon}_{\mathrm{L}}-1}\right\}. \qquad (4)$$

Independently of the direction of gaze, where $\dot{\varepsilon}_{\mathrm{R}}$ and $\dot{\varepsilon}_{\mathrm{L}}$ are, respectively, the angular velocities of the right and left retinal images, I is the interpupillary, separation, D is the viewing distance and $D \gg I$ (Beverley & Regan, 1973; Regan, 1993; Regan, Beverley, & Cynader, 1978). More generally, for motion within any meridian

$$\beta = \tan^{-1}\frac{I\dot{\alpha}}{D\dot{\delta}}, \qquad (5)$$

where $\dot{\delta}$ is the rate of change of retinal disparity relative to a fixed reference point (F), D is the distance of the object from the eye, and I is the interpupillary separation. The passing distance is given by

$$X_{\mathrm{p}} \approx \frac{I\dot{\alpha}}{\dot{\delta}}. \qquad (6)$$

(Regan, 1993). Eqs. (5) and (6) are also valid in the case of a fully cyclopean target created within dynamic random noise. Direction discrimination thresholds for such targets are precise (0.7 deg) and are similar to thresholds for a comparable dotted target that could be seen through either eye alone (Portfors-Yeomans & Regan, 1996). Note that for a fully cyclopean target Eqs. (3) and (4) are invalid, because the left and right images of the target do not exist.

Almost all previous research examining the use of the information sources expressed in Eqs. (1)–(6) has considered judgments of only the *relative* direction of MID. In these studies, observers judged which of two approaching objects was going more leftward or more upward for example. Psychophysical experiments of this type have shown that humans are sensitive to the information expressed in Eq. (1), and that discrimination

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[1] Bootsma and Peper (1992) provided indirect evidence that observers use Eq. (2) to estimate X_{p} (see also Peper, Bootsma, Mestre, & Bakker, 1994). Using approaching balls of different physical sizes it was shown that the passing distance at which subjects judged an approaching ball to be reachable increased with ball radius as predicted by Eq. (2).

threshold for an approaching object based on this optical variable is 0.12 deg or less (Regan & Kaushal, 1994). Similarly, it has been shown that humans are sensitive to the information expressed in Eqs. (3) or (5) and can use it to make precise (0.15–0.3 deg) discriminations of variations in the trajectory of a monocularly visible object approaching the head, though the directional discrimination threshold rapidly becomes less precise as the direction of motion becomes more oblique with respect to the head (Beverley & Regan, 1975; Portfors-Yeomans & Regan, 1997). For a monocularly visible object moving towards the observer within either the horizontal or vertical meridian there is evidence that information about the direction of MID is processed through four channels each of which prefers a different direction of MID,[2] and that the reason why directional discrimination threshold is so precise is that it is determined by the pattern of activity among these channels (Beverley & Regan, 1973; Beverley & Regan, 1975; Portfors-Yeomans & Regan, 1997). This is also the case for a fully cyclopean target created within dynamic visual noise (Regan et al., 1998). However, although these previous experiments demonstrated precise discrimination of binocular and monocular information about the direction of MID, precise discrimination of relative direction is only a necessary rather than a sufficient condition for accurate estimation of *absolute* direction (i.e., the judgment that is actually required when hitting or catching).

The main goal of the present study was to measure the accuracy of judgments of the absolute direction of MID with and without feedback. To expand on previous research we compared judgments based on monocular information alone, binocular information alone and a combination of binocular and monocular information. In the final set of experiments the identical visual stimuli were used in a simulated catching task (Gray & Sieffert, 2005). This permitted a direct comparison between the accuracy of the perception and the accuracy of a goal-directed action that was based on that perception. To address limitations of previous research on this topic (see Section 7.4) we dissociated task-relevant and task-irrelevant variables (Regan & Gray, 2000, 2004) so as to allow the relative contribution of task-relevant and task-irrelevant variables to be estimated by means of stepwise regression analysis.[3] We conclude that catching an approaching object requires that the result of *combined* visual processing and motor action should accurately guide the hand so that it is located at the same point in space as the ball at the instant that the ball arrives at this point. We suggest here that the marked improvement with practice in the catching performance of dedicated games players is largely or entirely brought about by adapting the motor action to errors in the visual representation of passing distance and time to passage (TTP).

2. Experiment 1: Accuracy of perception of the direction of motion-in-depth

2.1. Purpose

The purpose of Experiment 1 was to measure the accuracy of judging the absolute direction of MID when no feedback was provided and judgments were based on (a) monocular information alone, (b) binocular information alone, and (c) a combination of the two.

2.2. Apparatus

The simulated approaching object (a red sphere with no texture or shading) was displayed on a 28 cm vertical × 36 cm horizontal SVGA monitor (Viewsonic model PT795) with a screen resolution of 1024 × 768 pixels that ran at 120 Hz. The background was black. Two hundred randomly positioned small (0.1 deg diameter) white dots were presented above and below the simulated approaching object to provide reference marks for changes in relative disparity. The dots were arranged so at no point were they occluded by the simulated approaching object. The monitor was viewed from a distance of 180 cm in a dark room. Horizontal disparity between the left and right eye's images of the object was created using LCD shutter glasses (Stereographics Crystal Eyes). The object's initial size θ_0 (i.e., at time $t = 0$) was 1 deg and its initial retinal disparity was 0.5 deg uncrossed. The simulated physical size and initial distance of the object were held constant across trials. The initial position of the simulated object was always the center of the display (i.e., 0 deg off the midline). The simulated ball always traveled along a straight path. There were three different viewing conditions. For the "monocular" viewing condition, a sensation of motion towards the observer along different trajectories was created by increasing the angular size of the object as a function of time (θ_t) according to the following equation:

$$\theta_t = \tan^{-1}\left[\frac{\tan\theta_0}{1-\left(\frac{t}{TTP\cos^2\beta}\right)}\right] \tag{7}$$

and by changing the lateral angular position of the ball as a function of time (α_t) according to the equation

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[2] It is puzzling that analogous experiments failed to reveal evidence for channels in the processing of monocular information about the direction of MID (Regan, 1986).

[3] By "task-relevant variable" we mean here the variable that predicts the crossing distance (i.e., Eqs. (2), (4) or (6)). Clearly, to catch a ball reliably in everyday life a person's action must be based on a task-relevant variable. In laboratory psychophysical experiments, however, the experimental design commonly allows a participant to achieve successful responses on the basis of a task-irrelevant variable. A participant may not be aware that he or she is using such a stratagem, one which in everyday life would be generally unsuccessful.

$$\alpha_t = \frac{X_{\mathrm{p}}(\theta_t - \theta_0)}{2(\tan\theta_0)D}, \tag{8}$$

where TTP was the time to passage (i.e., the number of seconds remaining until the simulated approaching object would have crossed the frontal plane) and D was the viewing distance. For the "binocular" viewing condition, a sensation of motion towards the observer along different trajectories was created by increasing the relative retinal disparity of the object (δ_t) as a function of time according to the equation

$$\delta_t = \delta_0 + \frac{It}{D(\cos^2\beta(TTP - t))} \tag{9}$$

and by changing the lateral angular position of the ball (α_t) as a function of time according to the equation

$$\alpha_t = \frac{X_{\mathrm{p}}(\delta_t - \delta_0)}{I}. \tag{10}$$

For the "both" viewing condition, the angular size was increased according to Eq. (7) *and* the angular disparity was increased according to Eq. (9). The lateral angular position of the ball was changed according to Eq. (8). This viewing condition simulates the real-world situation in which both monocular and binocular information about X_{p} are available. The vertical position of the simulated object remained constant in all conditions. All observers reported a subjective impression of MID in all conditions.

As illustrated in Fig. 2, an array of 24 light-emitting diodes (LEDs) oriented parallel to the face of the monitor was positioned 15 cm in front of and 10 cm below the observer's eyes. The diameter of each LED was 0.2 cm. The spacing between adjacent LEDs was 1 cm (i.e., roughly 0.3 deg relative to the face of the monitor) center to center. Illumination of the LEDs was controlled by a National Instruments card (model PCI 1200).

2.3. Procedure

The procedure we used to measure perceived absolute direction of MID was analogous to the method we used in several previous studies to measure the perceived absolute time to collision (TTC) of an approaching object (e.g., Gray & Regan, 1998, 2000, 2000b). Three values of the initial angular speed of frontal plane motion $\dot{\alpha}_{t=0}$ were randomly interleaved with three values of either the initial rate of change of angular size $\dot{\theta}_{t=0}$ (monocular information only) or the initial rate of change of relative disparity $\dot{\delta}_{t=0}$ (binocular information only) or with a combination of $\dot{\theta}_{t=0}$ and $\dot{\delta}_{t=0}$ (combined monocular and binocular information).[4] Each of these three conditions gave the same nine different simulated trajectories. Presentation duration (PD) was chosen from one of nine values between 500 and 700 ms, randomly selected on each presentation. On each trial, the simulated object approached along one of the trajectories described below and then disappeared from the screen. At the instant when the simulated object would have collided with the LED array, one of the 24 LEDs in the array was illuminated for a duration of 1 s. The observer's task on each trial was to judge whether the simulated approaching object would have passed to the left or to the right of the illuminated LED and to indicate their choice by pressing one of the two response buttons. No feedback was provided. Extrapolation times (i.e., TTP-PD) ranged from 0.2 to 0.5 s.

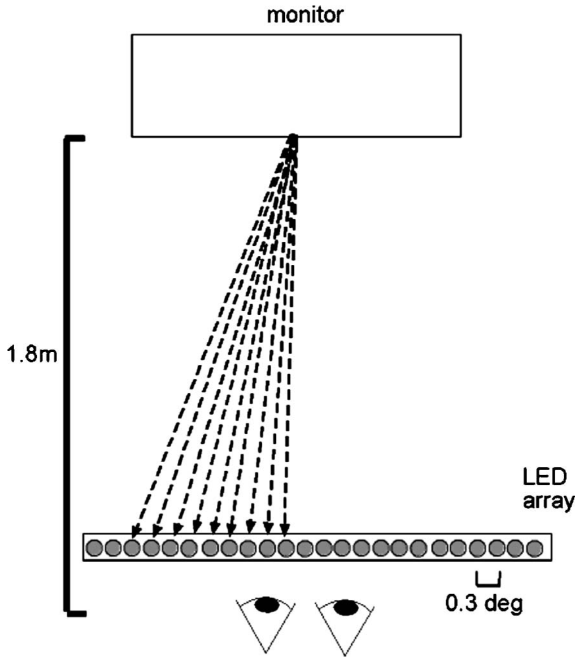

Fig. 2. Top view of the experimental setup. The observer viewed a simulated object that approached along one of nine different trajectories in depth (shown with dashed lines) chosen randomly. An array of 24 LEDs (gray dots) was positioned in front of the observer's eyes. At the instant when the simulated object would have collided with the LED array one of the LEDs in the array was illuminated. The observer's task on each trial was to judge whether the simulated approaching object would have passed to the left or to the right of the illuminated LED. The location of the LED that was illuminated was varied from trial to trial on the basis of the observer's previous button press using a staircase method. See text for details.

The location of the LED that was illuminated was varied from trial to trial on the basis of the observer's previous button presses using the simple 1-up, 1-down staircase method described by Levitt (1971). Consider the trajectory that passes furthest to the left of the observer's eyes in Fig. 2. If, for example, on the first presentation of that trajectory the LED in the center of the array was illuminated and the observer pressed the

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[4] Note that because we simulated straight-line trajectories the values of $\mathrm{d}\theta/\mathrm{d}t$, $\mathrm{d}\alpha/\mathrm{d}t$, and $\mathrm{d}\delta/\mathrm{d}t$ were not constant during the simulated approach, see Eqs. (7)–(10).

"left" button the position of the illuminated LED would be shifted to the left for the next presentation for that trajectory. This leftward shift would continue until the observer indicated that the perceived direction was to the right of illuminated LED (a reversal) at which point a rightwards shift of LED position would begin. For each run we randomly interleaved the nine staircases corresponding to nine different trajectories. The use of more than one staircase prevented observers from anticipating the location of the illuminated LED on the next trial and also improved the accuracy with which the resulting nine estimates could be compared. The particular staircase presented on each trial was chosen randomly. For any given run, all nine trajectories were in one half of the observer's visual field. Judgments for simulated objects passing to the right of the midline and object passing to the left of the midline were collected in separate runs.

For each of the staircases the initial step size was 0.6 deg, i.e., twice the distance between adjacent LEDs. Step size was halved after the first reversal. The position of the illuminated LED for the first presentation in each staircase was chosen randomly. Each experimental run was completed when at least four reversals (not including the first reversal) had occurred for all nine staircases (roughly 150 trials). The endpoint of each successive staircase was based on the final four reversals; all other reversals were ignored. Each staircase converged onto a LED location that gave a 50% probability that the observer would judge that the simulated approaching object would have passed to the left of that position. We took that position to indicate the perceived direction of MID. We varied $\dot{\alpha}_{t=0}$ and $\theta_{t=0}$ orthogonally in our experimental design allowed so that we could compare the contributions to the observer's responses of the task-relevant variable (i.e., β) and these two task-irrelevant variables (see Portfors-Yeomans & Regan (1997) for further details of this design). The variation of presentation duration allowed us to compare the contributions of the task-relevant variable β and the two task-irrelevant variables α_{final} and θ_{final} by partially dissociating these variables (described in more detail below). The values of $\dot{\alpha}_{t=0}$ used were 4, 5, and 6 deg/s. The values of $\dot{\theta}_{t=0}$ used were 1.5, 1.7, and 1.9 deg/s. The values of $\delta_{t=0}$ used were 0.9, 1.1, and 1.2 deg/s. The nine resultant trajectories were 6.7, 7.4, 8.3, 8.4, 9.2, 9.9, 10.4, 11.0, and 12.5 deg off the midline. Each trajectory coincided with the location of one of the LEDs in the array.

Each observer completed 20 repeats (10 with leftwards trajectories and 10 with rightwards trajectories) for each of the three viewing conditions (binocular information alone, monocular information alone and a combination of binocular and monocular information). Data for each of these three conditions were collected on separate runs with the order counterbalanced.

2.4. Data analysis

To check whether observers based their responses on the task-relevant variable β, we performed separate stepwise regression analyses for each of the three viewing conditions. For the monocular information alone condition, we used the task-relevant variable β and the following task-irrelevant variables: $\theta_{t=0}, \dot{\alpha}_{t=0}$, monocular time to collision [i.e., $\theta/\dot{\theta}$], presentation duration, θ_{final}, α_{final}, $\Delta\theta$, and $\Delta\alpha$ in the analysis. For the binocular information alone condition, we used the task-relevant variable β and the following task-irrelevant variables: $\delta_{t=0}, \dot{\alpha}_{t=0}$, binocular TTC [i.e., $I/D\dot{\delta}$], presentation duration, δ_{final}, α_{final}, $\Delta\delta$, and $\Delta\alpha$ in the analysis. For the "both" condition, all 13 of these task-irrelevant variables were included in the analysis. Correlations between β and the task-irrelevant variables were relatively low: ranging from 0.0 for $\theta_{t=0}$, and $\delta_{t=0}$ to 0.19 for θ_{final} to 0.45 for α_{final}.

Errors in judgments of the direction of MID were quantified by calculating the angular difference between the endpoint of the staircase for each trajectory and the value of β for that particular trajectory.

2.5. Observers

Six observers completed Experiments 1–5. All observers had normal or corrected to 6/6 visual acuity and results within the normal range for binocular vision, color vision, and phoria tests of the Optec Vision Tester (Stereo Optical, Chicago, IL). Observer 4 was authors B.R., and observer 5 was author R.G. The other four observers were naïve as to the aims of the experiment and performed the experiments for course credit. The order of Experiments 1–4 was chosen randomly for each observer. Experiment 5 was completed last by all observers.

2.6. Results

Table 1 shows the results of the stepwise regression analyses for all three viewing conditions used in Experiment 1. For the monocular information alone condition, the task-relevant variable β was by far the most significant variable and accounted for a large percentage of response variance (ranging from 84% to 94%) for all six observers. For the binocular information alone condition, the task-relevant variable was by far the most significant variable and accounted for a large percentage of response variance (ranging from 81% to 94%) for all six observers. For the condition in which both sources of information were available the task-relevant variable was by far the most significant variable and accounted for a large percentage of response variance (ranging from 79% to 90%) for all six observers. In contrast with the results reported by Harris and Dean (2003) we did not find that observer's response were primarily based

Table 1
R^2 values obtained from stepwise regression analysis of observers' responses in Experiment 1

Observer	Condition	Most significant variable	R^2	Next significant variable	R^2
Stepwise regression					
1	Monoc.	Eq. (2)	0.92	α_{final}	0.93
	Binoc.	Eq. (5)	0.81	$(d\theta/dt)_{t=0}$	0.85
	Both	Eqs. (2) and (5)	0.90	$(d\theta/dt)_{t=0}$	0.92
2	Monoc.	Eq. (2)	0.93	NA	NA
	Binoc.	Eq. (5)	0.91	$(d\theta/dt)_{t=0}$	0.92
	Both	Eqs. (2) and (5)	0.9	NA	NA
3	Monoc.	Eq. (2)	0.94	$(d\alpha/dt)_{t=0}$	0.95
	Binoc.	Eq. (5)	0.94	$(d\alpha/dt)_{t=0}$	0.95
	Both	Eqs. (2) and (5)	0.93	$(d\alpha/dt)_{t=0}$	0.94
4	Monoc.	Eq. (2)	0.85	NA	NA
	Binoc.	Eq. (5)	0.90	NA	NA
	Both	Eqs. (2) and (5)	0.80	NA	NA
5	Monoc.	Eq. (2)	0.92	NA	NA
	Binoc.	Eq. (5)	0.93	NA	NA
	Both	Eqs. (2) and (5)	0.82	Present duration	0.84
6	Monoc.	Eq. (2)	0.84	NA	NA
	Binoc.	Eq. (5)	0.89	NA	NA
	Both	Eqs. (2) and (5)	0.79	NA	NA

NA, not applicable because no other variables explained a significant amount of response variance.

Note. "Most significant variable" refers to the variable that accounted for the highest proportion of response variance. The R^2 value in the rightmost column is the total amount of response variance explained when both the most significant and next significant variable are added into the regression.

on the task-irrelevant variable α_{final}. For five of our six observers this variable did not account for any measurable response variance, and for the remaining observer only a very small proportion.

Figs. 3A–F show the mean MID direction judgment errors (averaged across all three sets of nine trajectories) for observers 1–6, respectively. Solid black bars are for monocular information alone (i.e., Eq. (1)), open bars are for binocular information alone (i.e., Eq. (5)), and solid gray bars are for the condition in which both information sources were available. Negative values indicate judgment errors towards the midline. From this figure it can be seen that in all but one case (the "both" condition in Fig. 3D) our participants perceived that the trajectory of the simulated approaching object was further from the midline than the trajectory indicated by the visual information provided. The overall mean errors for the monocular, binocular and "both" conditions were 2.6, 1.6, and 0.9 deg which are equivalent to misjudgments of crossing distance of 9.1, 5.6, and 2.8 cm. *t* tests revealed that in all three viewing conditions errors were significantly different from zero: monocular [$t(5) = 10.2$, $p < 0.001$], binocular [$t(5) = 8.6$, $p < 0.001$], and both [$t(5) = 3.1$, $p < 0.05$].

The errors of perceived direction were further analyzed using a 3 × 18 repeated measures ANOVA (with Greenhouse–Geisser correction) with viewing condition and trajectory as factors. Although the smallest mean error occurred in the condition in which both binocular and monocular information were available for all six observers, there was no significant effect of viewing condition on the error of perceived direction [$F(2,10) = 3.1$, $p > 0.05$]. There was also no significant effect of trajectory [$F(17,85) = 0.7$, $p > 0.5$] or a trajectory × condition interaction [$F(17,170) = 1.1$, $p > 0.1$].

2.7. Discussion

The results of stepwise regression analysis indicated that, in our particular laboratory conditions, observers based their responses on visual information that in the everyday world would have correlated with the direction of MID of an approaching rigid object. This suggests that we were not measuring an artifact of laboratory psychophysics, and encourages us that our findings would be valid in the everyday world as well as within the context of our particular laboratory psychophysical experimental design.

Our finding that the no-feedback binocularly based psychophysical estimates of the direction of MID are not accurate is unsurprising: since the deductive work of Tyler (1975) and certainly since the formal demonstration of Tyler's proposal by Regan, Erkelens, and Collewijn (1986a) it has been known that the perceived speed of illusory MID produced by a given rate of change of disparity depends strongly on the presence

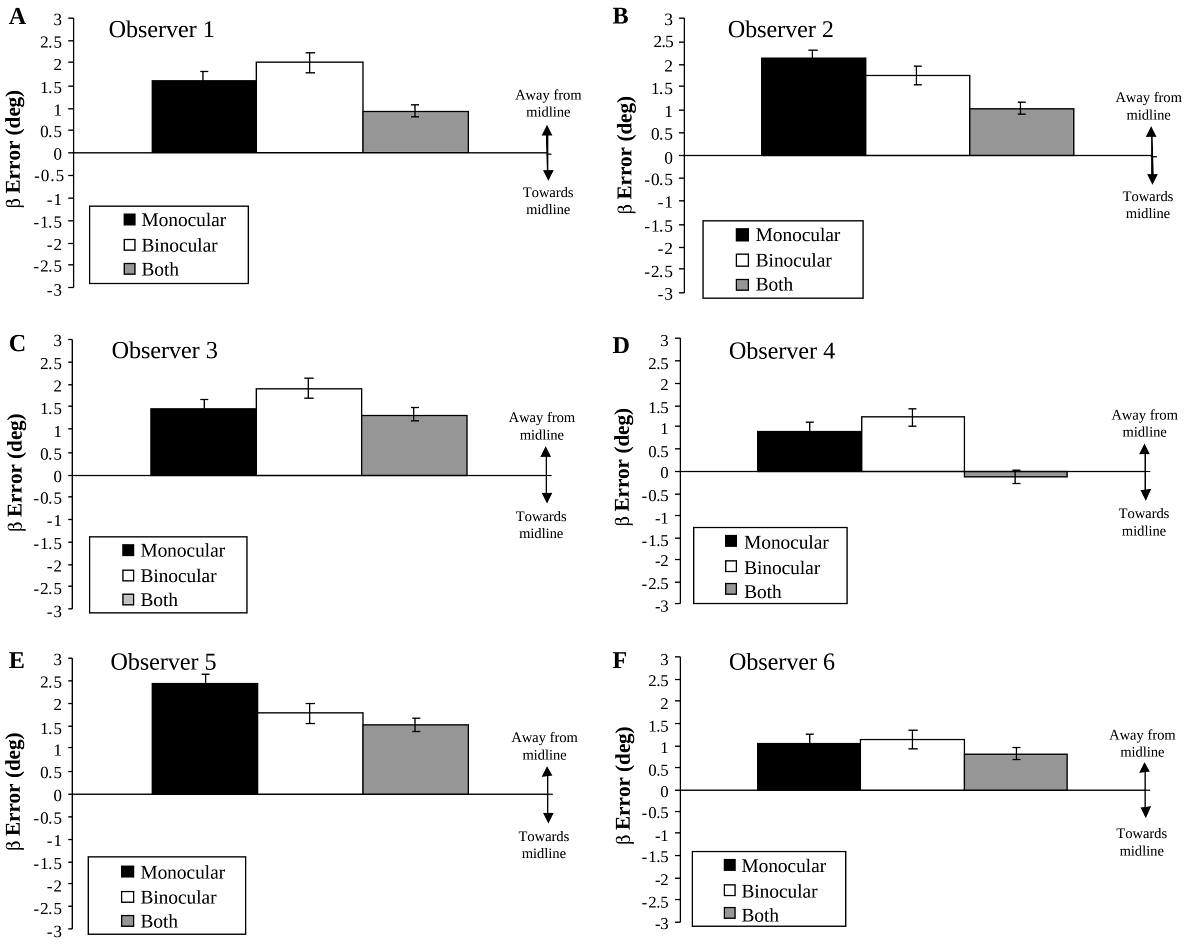

Fig. 3. Mean errors in judging the direction of motion in depth for observers 1–6 in Experiment 1 (no-feedback condition). Solid black bars are for monocular information alone (i.e., Eq. (1)), open bars are for binocular information alone (i.e., Eq. (5)) and solid gray bars are for the condition in which both information sources were available. Negative values indicate judgment errors towards the midline. Error bars show ±1 standard error. Means and standard errors are based on 180 data points.

and location of reference marks placed both across the visual field and in depth (Regan & Beverley, 1973) Perceived speed also depends on eccentricity of viewing and, for many otherwise normally sighted observers, on the presence of visual field areas that are specifically insensitive to MID produced by a rate of change of disparity. (Hong & Regan, 1989; Regan, Erkelens, & Collewijn, 1986b; Richards & Regan, 1973). In addition, the perceived speed of MID is not linearly proportional to the rate of change of disparity (Beverley & Regan, 1979; Regan & Beverley, 1973). Furthermore, although regions of the binocular visual field that produce little or no sensation of MID when stimulated by changing disparity alone have been reported to produce a normal sensation of MID when stimulated with a rate of change of size (Regan & Beverley, 1983), the perceived speed of MID produced by changing size is not linearly proportional to the rate of change of size (Beverley & Regan, 1979; Regan & Beverley, 1973) and falls off as viewing eccentricity is increased (Regan & Vincent, 1995). For whatever reason an attenuation in the perceived speed of MID produced by a given stimulus would be expected to shift the perceived trajectory wider with respect to the midline, and an increase in perceived speed would have the opposite effect.

The direction of the errors in the perception of MID direction that we found is consistent with previous research (Harris & Dean, 2003; Harris & Drga, 2005; Welchman, Tuck, & Harris, 2004). However, the magnitude of estimation errors were much smaller in the present study. Harris and Dean, 2003 reported a mean ratio of perceived to actual angle of roughly 6:1 when only binocular information was available. The equivalent ratio in the present study ranged from only 0.98:1 to 1.6:1 for the six observers.

In Experiment 1 there was no significant difference between the absolute accuracy of perceived direction for the three different viewing conditions. This finding is not consistent with our previous finding that judgments of the absolute TTC of an approaching object are significantly more accurate when estimates are based on a combination of monocular and binocular information compared to estimates based on either cue alone (Gray & Regan, 1998). Also evident from Fig. 3 is the fact that the relative performance in the monocular and binocular conditions was not consistent across our six observers. We return to this last finding in Experiment 5.

3. Experiment 2: Accuracy of psychophysical estimates of the direction of motion-in-depth when feedback is provided

3.1. Purpose

The purpose of Experiment 2 was to find the effect of feedback on errors in psychophysical estimates of direction of MID.

3.2. Apparatus and procedure

The apparatus and procedure were as described for Experiment 1 except that on each trial, the observer was given auditory feedback as to the accuracy of their judgments as follows. A high frequency (4000 Hz) tone was presented after each correct response while a low frequency (1000 Hz) tone was presented after each incorrect response. The tone duration was 1 second.

Each observer completed 20 repeats (10 with leftwards trajectories and 10 with rightwards trajectories) for each of the three viewing conditions (binocular information alone, monocular information alone and a combination of binocular and monocular information). Data for each of these three conditions were collected on separate runs with the order counterbalanced.

3.3. Results and discussion

Table 2 shows the results of the stepwise regression analysis for Experiment 2 data. As for Experiment 1, the task-relevant variable β was by far the most significant variable and accounted for a high percentage of response variance (ranging from 72% to 96%) in all condition for all six observers.

Figs. 4A–F show the mean direction judgment errors for observer 1–6, respectively. The pattern of results was similar to the "no feedback" conditions in Experiment 1. The overall mean errors for the monocular, binocular, and both viewing conditions were 1.3, 1.2, and 0.6 deg, respectively, which are equivalent to misjudgments of crossing distance of 4.1, 3.8, and 1.9 cm. Errors were significantly different than zero for all three viewing conditions: monocular [$t(5) = 8.2$, $p < 0.001$], binocular [$t(5) = 9.1$, $p < 0.001$], and both[$t(5) = 2.8$, $p < 0.05$].

Data for Experiments 1 and 2 were compared using a $2 \times 3 \times 18$ repeated measures ANOVA with Feedback Presence, Viewing Condition, and Trajectory as factors.

Table 2
R^2 values obtained from stepwise regression analysis of observers' responses in Experiment 2

Observer	Condition	Most significant variable	R^2	Next significant variable	R^2
Stepwise regression					
1	Monoc.	Eq. (2)	0.91	NA	NA
	Binoc.	Eq. (5)	0.87	θ_{final}	0.89
	Both	Eqs. (2) and (5)	0.90	$(\mathrm{d}\theta/\mathrm{d}t)_{t=0}$	0.92
2	Monoc.	Eq. (2)	0.96	NA	NA
	Binoc.	Eq. (5)	0.92	NA	NA
	Boths	Eq. (2) and (5)	0.92	NA	NA
3	Monoc.	Eq. (2)	0.94	$(\mathrm{d}\theta/\mathrm{d}t)_{t=0}$	0.95
	Binoc.	Eq. (5)	0.95	$(\mathrm{d}\theta/\mathrm{d}t)_{t=0}$	0.97
	Both	Eqs. (2) and (5)	0.93	$(\mathrm{d}\alpha/\mathrm{d}t)_{t=0}$	0.95
4	Monoc.	Eq. (2)	0.72	NA	NA
	Binoc.	Eq. (5)	0.81	NA	NA
	Both	Eqs. (2) and (5)	0.8	NA	NA
5	Monoc.	Eq. (2)	0.86	NA	NA
	Binoc.	Eq. (5)	0.81	NA	NA
	Both	Eqs. (2) and (5)	0.87	NA	NA
6	Monoc.	Eq. (2)	0.80	NA	NA
	Binoc.	Eq. (5)	0.88	NA	NA
	Both	Eqs. (2) and (5)	0.75	NA	NA

NA, not applicable because no other variables explained a significant amount of response variance.
Note. "Most significant variable" refers to the variable that accounted for the highest proportion of response variance. The R^2 value in the rightmost column is the total amount of response variance explained when both the most significant and next significant variable are added into the regression.

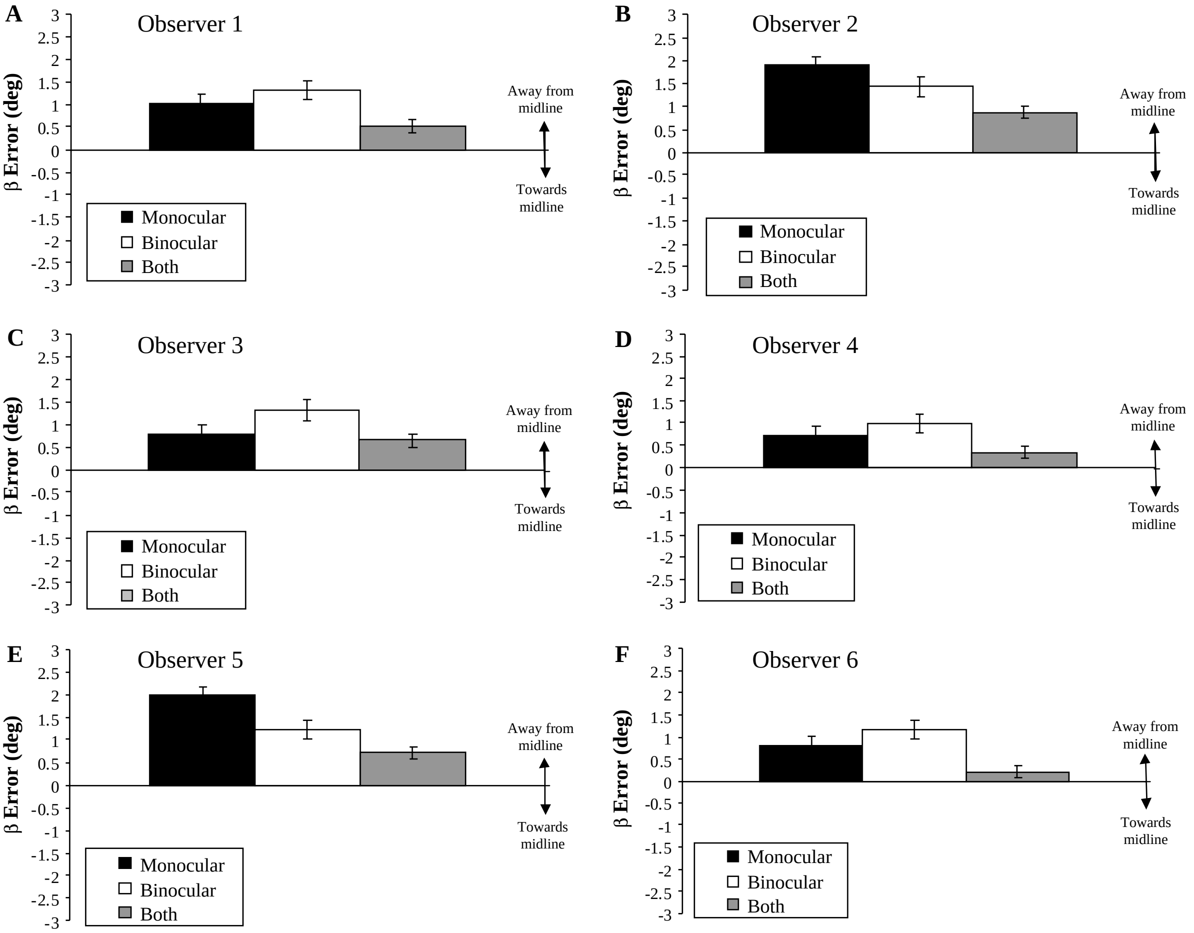

Fig. 4. Mean errors in judging the direction of motion in depth for observers 1–6 in Experiment 2 (with-feedback condition). Solid black bars are for monocular information alone (i.e., Eq. (1)) open bars are for binocular information alone (i.e., Eq. (5)), and solid gray bars are for the condition in which both information sources were available. Negative values indicate judgment errors towards the midline. Error bars show ±1 standard error. Means and standard errors are based on 180 data points.

This analysis revealed a significant overall effect of feedback [$F(1,5) = 7.2$, $p < 0.05$] with the mean error being significantly lower when feedback was present. The interaction between Viewing Condition and Feedback was not significant. The main effect of viewing condition and trajectory were not significant nor was there interaction.

Although the addition of auditory feedback resulted in an improvement in the accuracy of judging the direction of MID for all viewing conditions, errors were still significantly greater than zero. Our observers continued to judge the trajectories to be wider of the head than indicated by the visual information provided; they could not use feedback to accurately calibrate psychophysical responses (button presses in this case). It is possible that responses could have been accurately calibrated with additional practice however we feel this is unlikely given that each observer completed roughly 9000 trials in Experiment 2. And as will be shown below accurate calibration for the active task was exhibited with the same amount of practice.

4. Experiment 3: Accuracy of simulated catching with no-feedback

4.1. Purpose and rationale

The purpose of Experiment 3 was to use the simulated catching task developed by Gray and Sieffert (2005) to assess the spatial accuracy of interceptive hand movements based on monocular information alone, binocular information alone, and a combination of the two information sources. To allow for direct comparison with the psychophysical (button press) data we use the identical visual stimuli as were used in Experiments 1 and 2.

4.2. Apparatus

The visual display used in Experiment 3 was identical to that described for Experiment 1 except that the LED array was not present. Two Fastrack Polhemus motion tracking systems integrated with custom-designed software were used to track and digitally record motion kinematics. One Polhemus transmitter was attached to the lateral thumb of a glove made of stretchable material, and a second transmitter was attached to the index finger of the glove. The index finger and thumb were chosen for motion tracking as they were assumed to be the best indicators of grasping action. Motion of the hand was tracked at a sampling rate of 120 Hz from each transmitter. The estimated static positional precision of our tracking system (<0.2 mm) was derived from the standard deviation of 50 samples with the receivers at a constant position. The dynamic precision of the system (<1 mm) was estimated using the method described by Tresilian and Lonergan (2002). Feedback as to the accuracy of the catching movement was not provided.

4.3. Procedure

At the beginning of each trial, the participant placed the preferred hand (with the thumb and index finger together) on a fixed start position marked with a cross on a table in front of him or her. This start position was 180 cm distant from the face of the monitor directly below the eyes, and was 30 cm below the center of the monitor. Participants were instructed to keep their hand at the start position until the ball appeared on the screen and that they were to reach out and catch the simulated ball by moving their hand and adjusting their grasp. They were further instructed to move their hand laterally (perpendicular to the monitor) when catching and to try and avoid reaching forward towards the monitor. The inter-trial interval was 2 s. Prior to beginning the experiment participants completed 25 practice trials.

The method of constant stimuli was used to present the different trajectories of MID. The same nine trajectories used in Experiments 1 and 2 were presented in each of the three viewing conditions. On each run, the nine trajectories were each repeated five times for a total of 45 trials. Each observer completed three runs for each condition. As was the case for Experiment 1, data for leftwards trajectories and rightwards trajectories were collected on separate runs.

4.4. Data analysis

The grasping phase of the virtual catch was documented by measuring as a function of time the distance between the thumb and index finger. Previous research has shown that the timing of the closure of the hand is the aspect of the catching that is most strongly linked to variations in visual information (Gray & Sieffert, 2005; Hecht, Kaiser, Savelsbergh, & van der Kamp, 2002). In the present study, we defined this variable as the point in time and space such that the distance between the thumb and index finger first reached its minimum value. Since we were primarily interested in how simulated catching accuracy would compare to the estimates of the direction of MID within the horizontal plane measured in Experiment 1, the main variable used in our analyses was the lateral location of the hand at the instant when the hand closure occurred (CLOS_x) When calculating the catching error this variable was compared with the lateral position of the simulated ball at the instant when hand closure occurred (BALL_x).

To determine the relative contributions of the task-relevant (X_p) and task-irrelevant variables to simulated catching we performed stepwise regression analyses using the value of CLOS_x as the dependent variable, the task-relevant independent variables (Eqs. (2) and (6)) and the task-irrelevant independent variables described in Experiment 1.

4.5. Results

Table 3 shows the results of the stepwise regression analysis for Experiment 3 data. As in Experiment 1, the task-relevant variable X_p was by far the most significant variable and accounted for a high percentage of the total response variance (ranging from 68% to 90%) in all conditions for all six observers.

Figs. 5A–F show the mean value of CLOS_x–BALL_x (i.e., the lateral catching error) for observers 1–6, respectively. Solid black bars are for monocular information alone (Eq. (1)) open bars are for binocular information alone (Eq. (5)) and solid gray bars are for the condition in which both information sources were available. Positive values indicate that lateral position of the hand was further from the body midline than the lateral position of the simulated ball at the instant of hand closure.

The pattern of results is consistent with the errors of perceived trajectory found in Experiments 1 and 2: observers overreached when attempting to catch the simulated approaching ball, i.e., their hand was further away from the midline than the simulated object at the time of hand closure. The overall mean errors for the monocular, binocular, and both viewing condition were 2.2, 2.1, and 1.1 deg, respectively, which are equivalent to crossing distance errors of 6.9, 6.7, and 3.5 cm. Errors were significantly different from zero for all three viewing conditions: monocular only [$t(5) = 11.4$, $p < 0.001$], binocular only [$t(5) = 12.6$, $p < 0.001$], and both [$t(5) = 4.2$, $p < 0.05$].

Catching error data were further analyzed using a 3 × 18 repeated measures ANOVA with viewing condition and trajectory as factors. There was a significant effect of viewing condition [$F(2,10) = 5.2$, $p < 0.05$]. A post hoc comparison revealed that the mean catching error for the "both" condition was significantly smaller than the combined mean for the monocular and binocular conditions [$t(5) = 2.9$, $p < 0.05$]. The trajectory main effect and trajectory × viewing condition interaction were not significant.

Table 3
R^2 values obtained from stepwise regression analysis of observers' hand movements in Experiment 3

Observer	Condition	Most significant variable	R^2	Next significant variable	R^2
Stepwise regression					
1	Monoc.	Eq. (2)	0.82	NA	NA
	Binoc.	Eq. (5)	0.80	NA	NA
	Both	Eqs. (2) and (5)	0.77	$(\mathrm{d}\theta/\mathrm{d}t)_{t=0}$	0.8
2	Monoc.	Eq. (2)	0.83	NA	NA
	Binoc.	Eq. (5)	0.81	NA	NA
	Both	Eqs. (2) and (5)	0.84	α_{final}	0.86
3	Monoc.	Eq. (2)	0.69	NA	NA
	Binoc.	Eq. (5)	0.85	$(\mathrm{d}\theta/\mathrm{d}t)_{t=0}$	0.87
	Both	Eqs. (2) and (5)	0.77	$(\mathrm{d}\theta/\mathrm{d}t)_{t=0}$	0.81
4	Monoc.	Eq. (2)	0.90	NA	NA
	Binoc.	Eq. (5)	0.71	α_{final}	0.75
	Both	Eqs. (2), (5)	0.82	α_{final}	0.84
5	Monoc.	Eq. (2)	0.86	NA	NA
	Binoc.	Eq. (5)	0.80	$(\mathrm{d}\theta/\mathrm{d}t)_{t=0}$	0.86
	Both	Eqs. (2) and (5)	0.78	$(\mathrm{d}\theta/\mathrm{d}t)_{t=0}$	0.81
6	Monoc.	Eq. (2)	0.86	α_{final}	0.91
	Binoc.	Eq. (5)	0.76	NA	NA
	Both	Eqs. (2) and (5)	0.68	NA	NA

NA, not applicable because no other variables explained a significant amount of response variance.
Note. "Most significant variable" refers to the variable that accounted for the highest proportion of response variance. The R^2 value in the rightmost column is the total amount of response variance explained when both the most significant and next significant variable are added into the regression.

5. Experiment 4: Accuracy of simulated catching when feedback was provided

5.1. Purpose

The purpose of Experiment 4 was to determine the spatial accuracy of interceptive hand movements based on monocular information alone, binocular information alone, and a combination of the two information sources in the condition that participants were given feedback as to the success of their catching performance.

5.2. Apparatus and procedure

The apparatus and procedure were identical to that described for Experiment 3 except that feedback was provided as follows. At the instant when hand closure occurred, the lateral location of the simulated approaching ball (BALL_x) was recorded. If the value of BALL_x–CLOS_x was greater than +2 cm, a low (1000 Hz) tone was presented 0.5 s after the instant when CLOS_x occurred. This indicated to the observer than he/she overreached (i.e., the hand was further from the midline than the simulated ball) during simulated catching. If the value of BALL_x–CLOS_x, was less than −2 cm, a high (4000 Hz) tone was presented to indicate an underreach. If $-2\,\mathrm{cm} \geqslant (\mathrm{BALL}_x\text{–}\mathrm{CLOS}_x) \leqslant +2\,\mathrm{cm}$ no tone was played. Observers were instructed that no tone indicated a successful catch. The two cm value was chosen because it approximately half the simulated ball diameter.

5.3. Results

Table 4 shows the results of stepwise regression analysis for the Experiment 4 data. As for Experiments 1–3, the task-relevant variables (X_{p}) was by far the most significant variable, and also accounted for a high percentage of the total response variance (ranging from 65% to 90%) in all conditions for all six observers.

Figs. 6A–F show the mean value of CLOS_x–BALL_x (i.e., the lateral catching error) for observers 1–6, respectively. It is clear from this figure that the addition of auditory feedback considerably improved catching performance. It is also evident that there was no consistent reaching bias across observers. Errors for all three viewing condition were not significantly different from zero as revealed by two-tailed t tests: monocular [$t(5) = 1.2$, $p > 0.5$], binocular [$t(5) = 0.8$, $p > 0.5$] and both [$t(5) = 0.3$, $p > 0.5$]. Judgment error data were analyzed using a 3 × 18 repeated measures ANOVA with viewing condition and trajectory as factors. Neither of the main effects not the interaction were significant.

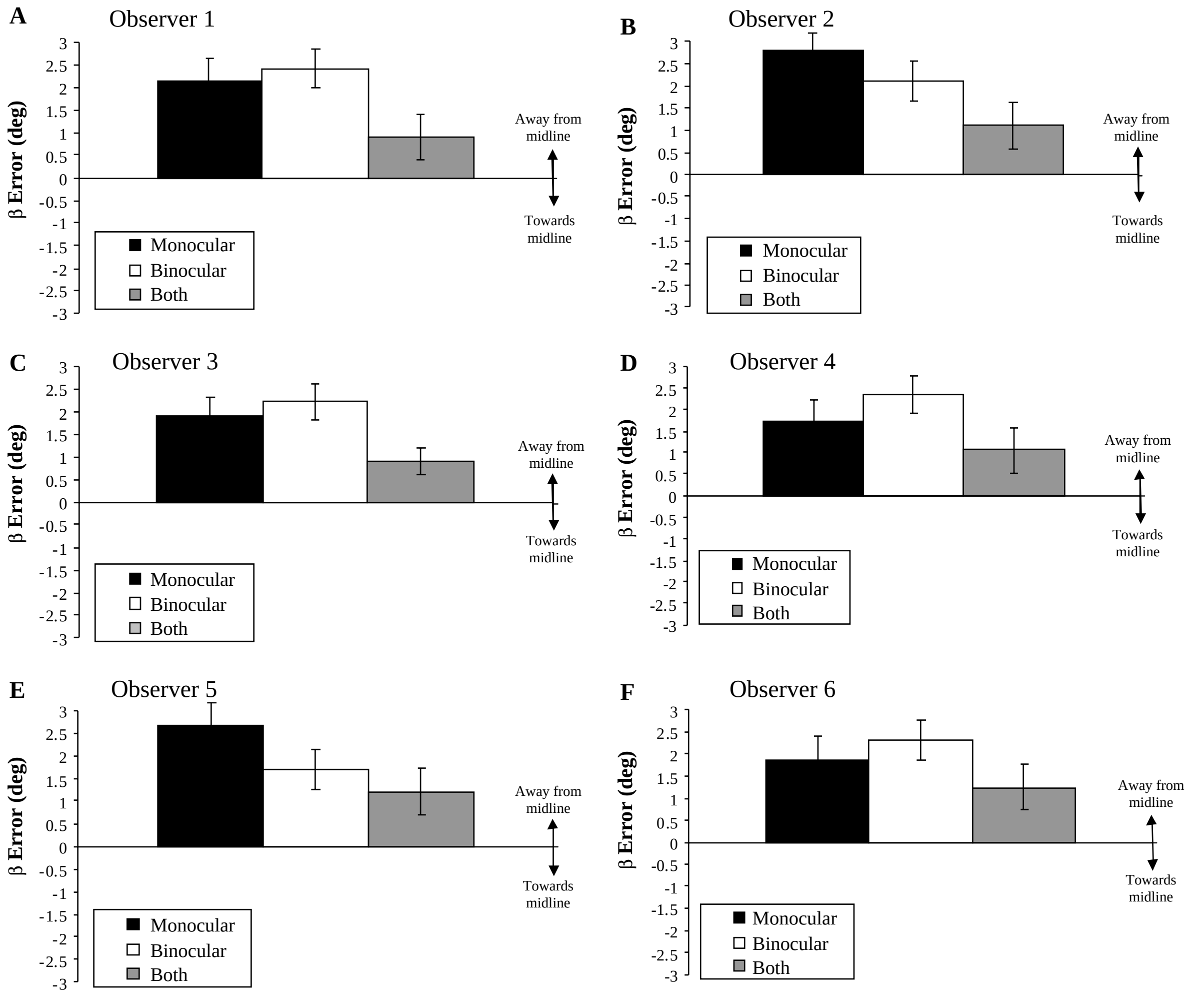

Fig. 5. Mean differences between the lateral position of the simulated ball (BALL_x) and the lateral position of the hand (CLOS_x) at hand closure in Experiment 3 (no-feedback condition). Solid black bars are for monocular information alone (i.e., Eq. (1)) open bars are for binocular information alone (i.e., Eq. (5)), and solid gray bars are for the condition in which both information sources were available. Negative values indicate judgment errors towards the midline. Error bars show ±1 standard error. Means and standard errors are based on 180 data points.

6. Experiment 5: Individual variations in the ability to use monocular and binocular information about trajectory

6.1. Purpose

Previous studies have reported large individual variations in the ratio between sensitivity to changing binocular disparity and sensitivity to changing angular size (Beverley & Regan, 1979). The purpose of Experiment 5 was to measure the ratio of sensitivity to changing disparity and changing size for each of the observers used in the present study, and to determine whether these ratios were related to the magnitude of errors in the different viewing conditions used in no-feedback Experiments 1 and 3.

6.2. Apparatus and procedure

To quantify sensitivities to superthreshold changing size and changing disparity we measured the perceived depth excursion for the following two different MID stimuli: (1) a rate of change of angular size of 1.9 deg/s, and (2) a rate of change of relative retinal disparity of 1.2 deg/s. The initial size of the stimulus was always 1 deg and the initial disparity was 0 deg. In all cases there was no lateral motion so that the object appeared to approach directly along the observer's midline. We used a modified version of the method used by Regan and Beverley (1973). Perceived depth excursion was measured using the method of adjustment as follows. The LED array used in Experiments 1 and 2 was oriented perpendicular to the monitor (as opposed to the parallel orientation used in Experiments 1 and 2). On each trial, one of the three stimuli described above was presented for a duration of 800 ms. Immediately after the approaching stimulus disappeared, one of the LEDs in the array was illuminated for a duration of 2 s (the display was blank during this interval). The initial position of the illuminated was chosen randomly from one of the 24 possible locations. Observers

Table 4
R^2 values obtained from stepwise regression analysis of observers' hand movements in Experiment 4

Observer	Condition	Most significant variable	R^2	Next significant variable	R^2
Stepwise regression					
1	Monoc.	Eq. (2)	0.87	NA	NA
	Binoc.	Eq. (5)	0.8	NA	NA
	Both	Eqs. (2) and (5)	0.75	NA	NA
2	Monoc.	Eq. (2)	0.90	NA	NA
	Binoc.	Eq. (5)	0.81	NA	NA
	Both	Eqs. (2) and (5)	0.85	α_{final}	0.87
3	Monoc.	Eq. (2)	0.72	NA	NA
	Binoc.	Eq. (5)	0.65	$(\mathrm{d}\theta/\mathrm{d}t)_{t=0}$	0.73
	Both	Eqs. (2) and (5)	0.75	$(\mathrm{d}\theta/\mathrm{d}t)_{t=0}$	0.82
4	Monoc.	Eq. (2)	0.88	NA	NA
	Binoc.	Eq. (5)	0.80	α_{final}	0.82
	Both	Eqs. (2), (5)	0.71	NA	NA
5	Monoc.	Eq. (2)	0.66	$(\mathrm{d}\theta/\mathrm{d}t)_{t=0}$	0.75
	Binoc.	Eq. (5)	0.72	$(\mathrm{d}\theta/\mathrm{dt})_{\mathrm{t}=0}$	0.80
	Both	Eqs. (2) and (5)	0.74	$(\mathrm{d}\theta/\mathrm{d}t)_{t=0}$	0.77
6	Monoc.	Eq. (2)	0.85	α_{final}	0.89
	Binoc.	Eq. (5)	0.87	NA	NA
	Both	Eqs. (2), (5)	0.88	α_{final}	0.93

NA, not applicable because no other variables explained a significant amount of response variance.
Note. "Most significant variable" refers to the variable that accounted for the highest proportion of response variance. The R^2 value in the rightmost column is the total amount of response variance explained when both the most significant and next significant variable are added into the regression.

controlled the position of the illuminated LED using the computer keyboard: pressing the up arrow made the illuminated LED move one position toward the monitor while pressing the down arrow made it move one position away from the monitor. Observers were instructed to adjust the position of the illuminated LED until it was at the same distance from the monitor as the simulated approaching object when it disappeared. After the LED was turned off the MID stimulus was presented again. This cycle continued until the observer pressed the space bar to indicate that he or she was satisfied with the setting. Each observer made 20 settings for each of the three viewing conditions.

6.3. Data analysis

To allow for comparison across experiments we first calculated the ratio of the perceived depth excursion in the Monocular condition to the perceived depth excursion in the Binocular condition (M/B ratio) for each observer. We then calculated the ratio of judgment errors in the monocular condition and the binocular condition for the no-feedback Experiments 1 and 3. We then calculated the correlation between these ratios.

6.4. Results and discussion

Table 5 shows the mean perceived depth excursions for the changing-size (i.e., monocular) and changing-disparity (i.e., binocular) stimuli. The M/B ratios calculated for the six observers from the Experiment 5 depth excursion data were positively correlated with the M/B ratios calculated from the judgment error data in Experiment 1 ($R = 0.71$, $p < 0.05$) and the M/B ratios calculated from the simulated catching error data in Experiment 3 ($R = 0.62$, $p < 0.05$).

Consistent with the findings of Regan and Beverley (1979) we found that our observers varied substantially in their relative sensitivity to changing size and changing disparity. This relative sensitivity could partially explain individual differences in performance for both absolute judgments of the direction of MID and simulated catching.

7. General discussion

7.1. The role of feedback in the accuracy of the perceived direction of motion-in-depth and the control of interceptive action

In previous papers we have argued that successful interceptive actions and collision avoidance are achieved by predicting *where* an approaching object will be at some future instant (*when*), and that this prediction is based on ratios of retinal image variables that correlate reliably with an approaching object's direction of MID and TTP or TTC (e.g., Beverley & Regan, 1973, 1975;

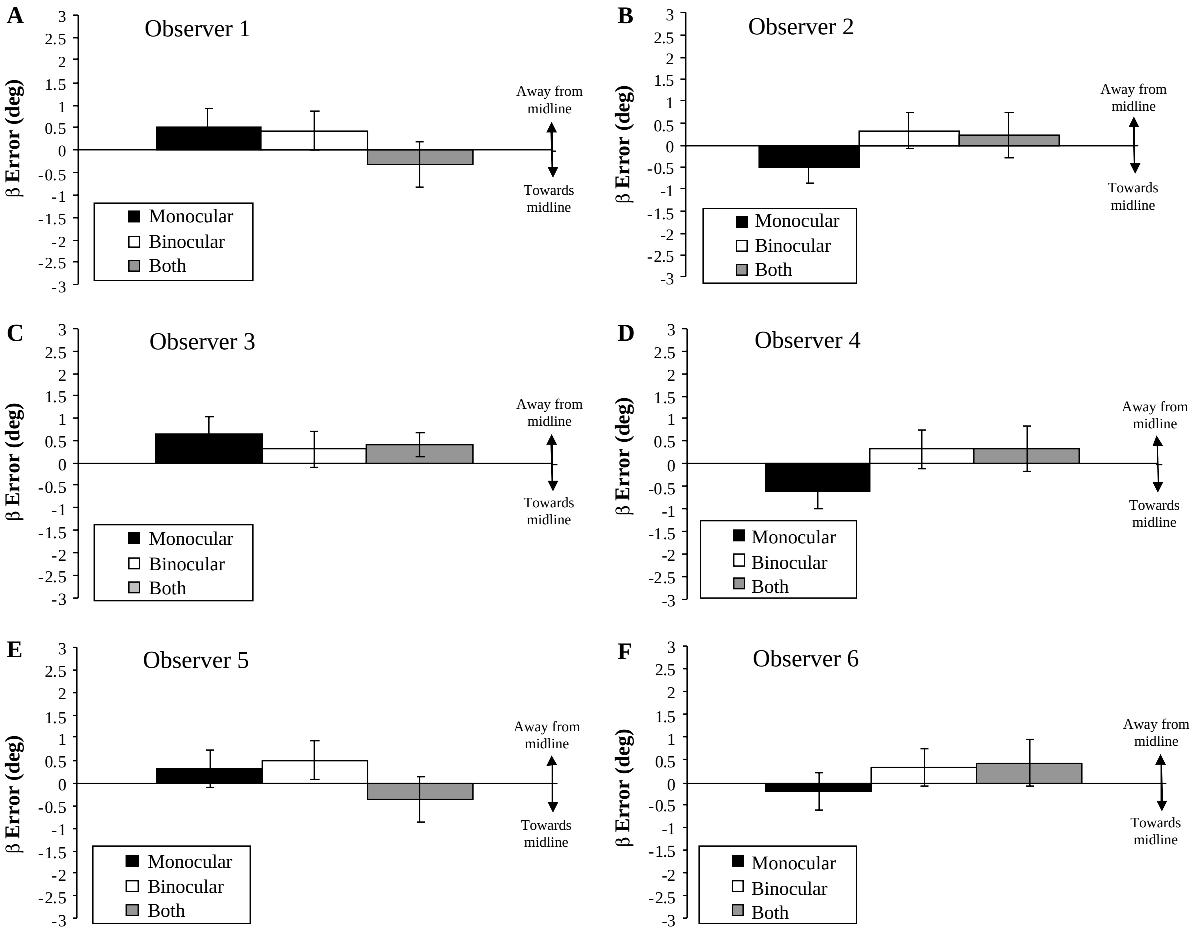

Fig. 6. Mean differences between the lateral position of the simulated ball (BALL$_x$) and the lateral position of the hand (CLOS$_x$) at hand closure in Experiment 4 (with–feedback condition). Solid black bars are for monocular information alone (i.e., Eq. (1)), open bars are for binocular information alone (i.e., Eq. (5)) and solid gray bars are for the condition in which both information sources were available. Negative values indicate judgment errors towards the midline. Error bars show ±1 standard error. Means and standard errors are based on 180 data points.

Gray & Regan, 1998; Kruk & Regan, 1983; Regan, 1992; Regan & Beverley, 1978; Regan & Gray, 2000, 2004; Regan, Beverley, & Cynader, 1979).[5] We report here that all our participants based their psychophysical (button press) responses on retinal image information that, in the everyday world, would correlate with the direction of MID (Eqs. (1) and (5)). Similarly, all our participants based their hand position at the instant of hand closure when "catching" a simulated approaching ball on retinal image information that, in the everyday world, would correlate with the passing distance (Eqs. (2) and (6)). Retinal image information that in the everyday world (as distinct from some laboratory conditions, see Section 7.4) would not correlate reliably with the direction of MID or with the passing distance was ignored.

Table 5
Mean perceived depth excursions (in cm) from Experiment 5

Observer	Changing size	Changing disparity
1	4.3	5.6
2	6.2	4.9
3	3.9	4.2
4	4.1	5.2
5	5.5	5.0
6	3.2	3.7

Our main finding concerns the effect of feedback on the accuracy of both psychophysical button presses

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[5] Alternatively, Peper et al. (1994) have proposed that in catching a ball that is passing wide of the head the catcher does not predict *where* and *when* on the basis of Eqs. (1)–(6). Rather, the catcher uses the monocularly available information set out in Eq. (12) to guide the velocity of the moving head in such a way that it is in the right place at the right time.

$$\frac{(\mathrm{d}D/\mathrm{d}t)}{D} = \frac{(\mathrm{d}\theta/\mathrm{d}t)}{\sin\theta} - \frac{(\mathrm{d}\gamma/\mathrm{d}t)}{\tan(\mathrm{d}\gamma/\mathrm{d}t)}, \tag{11}$$

where D is the current distance between the moving object, and P and γ is the angular subtense (from the viewpoint of the observing eye) of D. According to this line of thought the "right place" is not predicted; it is not known until the hand arrives there (see Montagne, Laurent, Durey, & Bootsma, 1999).

and of interceptive action. Our no-feedback psychophysical data indicated that the perceived direction of MID consistently differed from the direction indicated by the visual information provided, whether the information provided was monocular or binocular or a combination of the two. Feedback did improve the accuracy of psychophysical button presses, but errors remained. As to the question whether feedback caused the *perceived* direction of MID to change or merely altered the relationship between perception and button presses in much the same way as one might "aim off" with an inaccurately sighted rifle: the design of a rigorous psychophysical approach to this question is not immediately obvious since psychophysics, by definition, requires some form of motor response.

In the simulated catching task without feedback, the passing distance was judged inaccurately along the lines of the perceptual data. However, when feedback was introduced all participants made accurate catching judgments of the passing distance.

Our proposed explanation for the difference between results for the with-feedback perceptual task and the with-feedback simulated catching task is as follows. We assume that the ability to perform a particular visually guided action is developed by repeated attempts to achieve that action, the degree of failure to achieve the desired result providing feedback on each successive attempt, and that the combined visual processing and motor system are progressively modified by the feedback until the ability to perform the particular visually guided action is developed. In the particular example of visually guided catching, very many individuals will have gone through this process during early life, perhaps over years, until reliable catching performance had been achieved to a greater or lesser extent.

In our perceptual task participants pushed a button to signal whether they perceived the simulated approaching ball to pass to the left or to the right of an illuminated LED. We have no reason to suppose that our findings would have been different if participants had signaled their perceptual judgment by, for example, saying "left" or "right". We suggest that the motor component of the catching task was special in that catching with one's hand is a visually guided motor action that is progressively developed in early life so as to achieve reliable interception, while the button press in the perceptual task presumably had no relation to visually guided motor development an any of our participants' previous visuo-development history.

It is certainly possible that, given sufficient practice with feedback, our participants might have developed the ability to signal accurate judgments of the direction of MID by button presses (or verbal responses). After all, accomplished squash players reliably hit a fast-moving ball with the rather small "sweet spot" near the centre of the racquet, some 40 cm from the hand, and accomplished tennis cricket, and baseball players have a similar skill. However, the achievement of these skills requires long practice with feedback as to the outcome of action.[6]

7.2. Some requirements for reliably successful use of the where/when prediction stratagem for interceptive action and collision avoidance

If the where/when prediction stratagem is to support reliable performance, several conditions must be satisfied. Consider, for example, Eqs. (5) and (6). If the mechanism whose output signals the ratio between the approaching object's angular velocity parallel to the frontal plane ($d\alpha/dt$) and its rate of change of relative disparity ($d\delta/dt$) is fed by one filter specifically sensitive to $d\alpha/dt$ and a second filter specifically sensitive to $d\delta/dt$, then it is necessary that these two filters should operate independently of one another. In support of this requirement it has been reported that for variations of up to at least 2:1 in the direction of MID [signaled by variations in the ratio $(d\alpha/dt)/d\delta/dt$] and simultaneous variations in $d\delta/dt$ can be dissociated with 3% crosstalk, and variations in $d\delta/dt$ can be dissociated from simultaneous variations in the direction of MID with less than 1% crosstalk (Fig. 6 in Portfors-Yeomans & Regan, 1997). In addition, variations in the direction of MID can be dissociated from simultaneous variations in $d\alpha/dt$ with no measurable crosstalk (Table 2 in Portfors-Yeomans & Regan, 1997). Turning to Eqs. (1) and (2), $d\alpha/dt$ and the approaching object's rate of increase of angular subtense ($d\theta/dt$) are processed essentially independently providing that the object's retinal image is subject to noisy positional jitter such as that provided by an unsupported head as is typical outside the laboratory. Independence fails only when the head is supported on a headrest or bite bar. This requirement results from a nonlinearity in the visual mechanism sensitive to $d\alpha/dt$ and is an example of how noise can improve the operation of a visual mechanism by reducing the effect of an essential nonlinearity (Regan & Beverley, 1978, 1980). As to the TTC with a rigid spherical approaching object (TTC), where

$$TTC \approx \frac{\theta}{(d\theta/dt)}. \tag{12}$$

(Hoyle, 1957; Lee, 1976), the mechanism sensitive to ratio $\theta/(d\theta/dt)$ is independent of both angular

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[6] Furthermore, the calibration of the visuo-motor system seems to decay with time. At the start of the cricket season even professional players practice catching using a cradle device that, when a ball is thrown hard into it, causes the ball to fly towards the catcher along an unpredictable trajectory. Accurate placement of the hand and fingers is particularly important in cricket, where a fast-moving hard ball is caught with the unprotected hand.

subtense (θ) and of its rate of increase ($d\theta/dt$) (at least for small variations of θ and $d\theta/dt$) to within 1%, providing that the approaching object is viewed in central vision (Regan & Hamstra, 1993; Regan & Vincent, 1995).

Reliable interceptive action and collision avoidance is, however, not so easily explained. If, in everyday life, humans base such actions on Eqs. (1)–(6) that set out reliable retinal image correlates of both the direction of MID and of passing distance, they must allow for the fact that humans do not have direct access to the retinal image correlates set out in Eqs. (1)–(6), but only to the physiological responses to those retinal image correlates. This fact has several consequences. For example, as noted earlier, not only does the proximity to the object's retinal image of reference marks have a large effect on the perceived speed of MID produced by a given rate of change of relative disparity, but in addition the binocular visual fields of many individuals contain areas with reduced sensitivity to a rate of change of disparity. For any oblique trajectory, the greater the reduction in the perceived speed of MID, the wider of the head would the trajectory be perceived, even though the trajectory remained constant (see Eqs. (5) and (6)). A further problem is that the dynamic characteristics of the three filters that are sensitive, respectively, to changing disparity ($d\delta/dt$), to changing size ($d\theta/dt$) and to velocity within a frontoparallel plane ($d\alpha/dt$) are not identical (Beverley & Regan, 1979; Regan & Beverley, 1973). In principle, this carries the following implications: even if the direction of MID (β) were held constant in Eq. (1), the perceived direction would vary for sufficiently large yoked variations of $d\alpha/dt$ and $d\theta/dt$; even if direction of MID were held constant in Eq. (5), the perceived direction would vary for sufficiently large yoked variations of $d\alpha/dt$ and $d\delta/dt$. Therefore, for a rigid sphere approaching at constant speed along a straight-line oblique trajectory, the perceived direction of MID would be affected by sufficiently large differences in its linear speed and its distance. This prediction does not seem to have been tested for large variations of retinal image variables (thought, as mentioned earlier, it has been reported that variations of up to 2:1 have very little effect).

Turning from visually guided interceptive action to its converse, collision avoidance, we noted that the very recent past (in evolutionary terms) has seen demands on visually guided action that humans had not previously experienced, and that these recent demands strain the effectiveness of the *where/when* predictive stratagem (Gray & Regan, 2000a). For example, to safely overtake a slowly moving vehicle on a two-lane highway, a driver must estimate both the time to passage and the direction of MID relative to his or her vehicle for the vehicle to be overtaken and also for any oncoming vehicle. The *where/where* predictive collision avoidance strategy can be compromised by the *closing speed adaptation effect*:[7] if a driver looks straight ahead at the road, the radial flow of contours reduces the sensitivity of filters fed from the fovea that are specifically sensitive to rate of expansion (Regan & Beverley, 1978, 1979)[8] with the result that TTC or time to passage is overestimated (Gray & Regan, 1999, 2000a). Using a driving simulator we obtained evidence that this effect causes misjudgments in overtaking that have the potential to cause rear-end collisions, head-on collisions, and misjudgments when turning across oncoming traffic (Gray & Regan, 2005).[9] We predict here that adaptation of filters sensitive to rate of expansion would have a second consequence: Eq. (1) indicates that the direction of MID based on monocular information would be misperceived. This potentially hazardous possibility does not seem to have been investigated.

7.3. Predicting performance in everyday visually guided interceptive action and collision avoidance

It has been proposed that the visual component of performance in the everyday tasks of intercepting an approaching object (e.g., catching, tennis, and baseball) and of collision avoidance (e.g., driving and aviation) is largely determined by a small set of independently functioning parallel filters including those selectively sensitive to changing angular size and changing disparity (Regan, 1992; Regan & Gray, 2000, 2004; Regan et al., 1979). This hypothesis implies that the relative sensitivity of these filters (measured in simple laboratory tests) across individual has predictive value for individual differences in the performance of complex visually guided motor tasks such as driving or piloting an aircraft. In support of this hypothesis, correlations have been reported

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[7] Closing speed adaptation (Gray & Regan, 1999) is quite distinct from the familiar perceived reduction of one's forward speed experienced after a few minutes of high-speed road travel. The first effect is caused by a desensitization of changing-size filters (also called looming detectors), while the second effect is a desensitization of filters sensitive to unidirectional retinal image motion. These two kinds of filters each function almost completely independently of the other (Regan & Beverley, 1978, 1980). Adaptation of changing-size filters affects perceived TTC whether the TTC estimate is based on monocular information or binocular information (Gray & Regan, 1999). This is because monocular and binocular information about closing speed converge before the stage at which the MID signal is generated (Beverley & Regan, 1979). The effect of perceived TTC is large, up to 27% for monocularly based estimates and 16% for binocularly based estimates. These are overestimates, i.e., in the dangerous direction.

[8] The desensitization of changing-size filters can be caused by a radially expanding flow pattern that has a sufficiently large value of div V at its focus of expansion, where div V is the divergence of retinal image velocity (Regan & Beverley, 1979).

[9] In the USA alone road accidents accounted for 41,709 killed and 3.51 million injured in 1996, a typical year's toll (NHSTA, 1996). Some 15% of injury-causing road accidents in the UK involved overtaking (Jeffcote, 1973).

between, on the one hand, pilot performance in real high-performance jet aircraft as well as in simulators and, on the other hand, responses to changing-size stimuli and discrimination thresholds for the speed of a radially expanding flow pattern (Kruk & Regan, 1983; Kruk & Regan, 1996; Kruk, Regan, Beverley, & Longridge, 1981). In addition, as mentioned earlier, overestimates of time to collision produced by adapting to changing size were correlated with delays in the initiation of overtaking a lead vehicle in a car simulator (Gray & Regan, 2000a), and with misjudgments when turning across oncoming traffic (Gray & Regan, 2005).

The findings of our Experiment 5 provide further support for the hypothesis that individual differences in skilled visually guided interception can be at least partially predicted by individual differences in the sensitivities of the relevant filters (in this case filters for changing size and changing disparity). These findings along with the previous work of Regan and colleagues suggest that simple laboratory tests might be used to pre-screen individuals for skilled tasks of visually guided action as encountered, for example, in driving and flying.

7.4. Comparison with previous research on judgments of the absolute direction of motion-in-depth

There have been many published studies on the accuracy with which observers predict *when* an approaching object will collide with an observer (i.e., the absolute TTC) and the precision with which different values of TTC can be discriminated from each other. In contrast, reports on *where* an approaching object will be at some future time have almost entirely been restricted to documenting the high precision with which observers can discriminate between different directions of MID. There are comparatively few reports on an observer's accuracy in predicting the direction of MID or the passing distance. To our knowledge the only reports on the accuracy with which observers judge the direction of MID are those published by Harris and colleagues (Harris & Dean, 2003; Harris & Drga, 2005; Welchman et al., 2004). These authors concluded that observers cannot accurately estimate the direction of MID. They proposed that observers do not use the retinal image information that, in everyday life, signals the direction of MID. Rather, they base their judgments on the angle between the instantaneous direction of an approaching object and the direction that the observer faces, even if this causes them to make systematic errors.[10]

The results reported here conflict with the conclusions of Harris and colleagues. All our observers based their judgments in all six experimental condition on visual information that, in everyday life, signals the absolute direction of MID. Even without feedback, all our observers could predict the absolute direction of MID with far smaller errors than those reported by Harris and colleagues on the basis of monocular information alone, binocular information alone and with combined monocular and binocular information. When feedback was provided, estimates were accurate for the simulated catching test. Possible reasons for these disagreements are discussed next.

Harris and Dean (2003) reported the results of four experimental tasks. Task #1 required participants to draw the perceived trajectory on a piece of paper (as if the experimental setup was viewed from overhead). Task #2 required participants to rotate a pointer mounted on a table so that its angle matched the perceived trajectory. Task #3 required participants to give a yes/no verbal response to indicate whether the simulated approaching object would have contacted the participant's head. Task #4 required participants, immediately after the object disappeared, to move their finger along a bar mounted perpendicular to the plane of the monitor so as to indicate the location at which the simulated object would have passed over the bar. For all of these tasks it was found that the trajectory was judged to be wider of the head than was indicated by the visual information provided, though judgment precision was high, consistent with previous research using relative discrimination tasks (Beverley & Regan, 1973; Portfors-Yeomans & Regan, 1997). On the basis of these findings Harris and Dean (2003) concluded that human observers cannot use binocular information alone to judge accurately the direction of MID.

It is not clear that the conclusions of Harris and Dean (2003) are generally valid. Both the drawing and pointer Tasks (#1 and #2) used by Harris and Dean required a transformation of the coordinate system (from head-on to overhead). This requirement created a potential source of error. A failure to perform accurately either the drawing or the pointer tasks does not necessarily predict a failure to perform the quite different task of successfully catching a ball. Task #3 (judging whether the simulated approaching object would have hit the observer's head) provided only a crude estimate of judgment accuracy. Even Task #4 differed from the everyday act of catching, because it required the movement to be initiated after the simulated approaching object had passed the participant's head.

A further problem is that the stimulus variations used by Harris and Dean did not allow a determination of the relative contributions to the observers' responses of task-relevant and task-irrelevant variables (see Gray & Regan, 1998, Portfors-Yeomans & Regan, 1997, and

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[10] Though not discussed by Harris and colleagues, it was reported in previous studies of the discrimination of the direction of MID that all observers based their responses essentially entirely on visual information that, in everyday life, signals the direction of MID and that they ignored trial-to-trial variations in all other variables (Portfors-Yeomans & Regan, 1996, 1997).

Regan & Gray, 2004 for a detailed discussion of this issue). To determine whether observers can use Eq. (3) alone, i.e., the task-relevant visual information, to judge the direction of MID it is necessary to ensure that responses are not based on task-irrelevant variables such as the total change of relative disparity during the arbitrary stimulus presentation duration ($\Delta\delta$), the disparity of the approaching object when it disappears from the screen at the end of the trial (δ_{final}), the angular speed of translational motion across the retina ($d\alpha/dt$), and the lateral location of the simulated object when it disappears form the screen at the end of the arbitrary presentation duration (α_{final}). In everyday life reliably successful interception of an oncoming object could not be based on any of these task-irrelevant variables. In the Harris and Dean (2003) experimental designs, one or more task-irrelevant variables was correlated with the task-relevant variable. The rate of change of disparity ($d\delta/dt$) and α_{final} were both perfectly correlated with β (Eq. (5)). This created the undesirable situation that observers could, in principle, produce consistent responses based entirely or in part on the task-irrelevant variable, e.g., in Task #3 by indicating "no", the object will not hit my head for every trial in which $d\alpha/dt$ is above some critical value, or by adjusting the end of the pointer so that it was aligned with α_{final} in Task #2. If observers had adopted this strategy they may exhibit high precision but poor accuracy in their direction judgments, since such task-irrelevant variables do not accurately signal the direction of MID. This was the pattern of results reported by Harris and Dean (2003). Noting that this lack of stimulus variation might be problematic, Harris and Dean carried out a final experiment in which $d\delta/dt$, $\Delta\delta$, and δ_{final} were all perfectly correlated with the task-irrelevant variable (β) (Eq. (5)). This final experiment indicated that, for all conditions, observers based their "direction of MID" judgments on the value of α_{final} rather than the actual direction β: the estimated trajectory was roughly the same for all conditions in which α_{final} was the same, even though quite different directions of MID were simulated. We do not consider it valid to conclude that accurate judgment of the direction of MID cannot in general be made on the basis of information that correlates with the direction of MID from an experiment in which observers based their responses on something other than the direction of MID (in this case the lateral location of the target at the end of the arbitrary presentation duration).

Welchman et al. (2004) recently used a modified version of the pointer task described above (i.e., Task #2) to investigate the accuracy of absolute MID direction judgments for real and simulated approaching objects. In this study, participants rotated a pointer arm (that pivoted around the initial position of the object) to correspond to the perceived trajectory. In this study, both monocular and binocular cues to MID were present. Results were similar to those reported by Harris and Dean (2003) as observers produced large overestimates of the absolute direction of MID for both the simulated and the real object (see also Harris & Drga, 2005, for a more recent study using the pointer task).

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References

Beverley, K. I., & Regan, D. (1973). Evidence for the existence of neural mechanisms selectively sensitive to the direction of movement in space. *Journal of Physiology, 235*, 17–29.

Beverley, K. I., & Regan, D. (1975). The relation between discrimination and sensitivity in the perception of motion in depth. *Journal of Physiology, 249*, 387–398.

Beverley, K. I., & Regan, D. (1979). Separable after-effects of changing-size and motion-in-depth: Different neural mechanisms? *Vision Research, 19*, 727–732.

Bootsma, R. (1991). Predictive information and the control of action: What you see is what you get. *International Journal of Sports Psychology, 22*, 271–278.

Bootsma, R., & Peper, C. E. (1992). Predictive visual information sources for the regulation of action with special emphasis on hitting and catching. In L. E. Proteau (Ed.), *Vision and motor control*. Amsterdam: Elsevier.

Gray, R., & Regan, D. (1998). Accuracy of estimating time to collision using binocular and monocular information. *Vision Research, 38*(4), 499–512.

Gray, R., & Regan, D. (1999). Adapting to expansion increases perceived time-to collision. *Vision Research, 39*(21), 3602–3607.

Gray, R., & Regan, D. (2000). Estimating the time to collision with a rotating nonspherical object. *Vision Research, 40*(1), 49–63.

Gray, R., & Regan, D. (2000a). Risky driving behaviour: A consequence of motion adaptation for visually guided motor action. *Journal of Experimental Psychology: Human Perception and Performance, 26*(6), 1721–1732.

Gray, R., & Regan, D. (2000b). Simulated self-motion alters perceived time to collision. *Current Biology, 10*(10), 587–590.

Gray, R., & Regan, D. (2005). Perceptual processes used by drivers during overtaking in a driving simulator. *Human Factors, 47*, 394–417.

Gray, R., & Sieffert, R. (2005). Different strategies for using motion in depth information in catching. *Journal of Experimental Psychology: Human Perception and Performance*, in press.

Harris, J. M., & Dean, P. J. A. (2003). Accuracy and precision of binocular 3-D motion perception. *Journal of Experimental Psychology: Human Perception and Performance, 29*, 869–881.

Harris, J. M., & Drga, V. F. (2005). Using visual direction in three-dimensional motion perception. *Nature Neuroscience, 8*(2), 229–233.

Hecht, H., Kaiser, M. K., Savelsbergh, G. J. P., & van der Kamp, J. (2002). The impact of spatiotemporal sampling on time-to-contact judgments. *Perception Psychophysics, 64*(4), 650–666.

Hecht, H., & Savelsbergh, G. J. P. (2004). *Theories of time-to contact*. Amsterdam: Elsevier.

Hong, X., & Regan, D. (1989). Visual field defects for unidirectional and oscillatory motion in depth. *Vision Research, 29*, 809–819.

Hoyle, D. (1957). *The black cloud*. Harmond & Worth: Penguin, pp. 26–29.

Jeffcote, G. O. (1973). Analysis of national statistics of overtaking accidents. In *International drivers behaviour research association report*. UK: University of London.

Kruk, R., & Regan, D. (1983). Visual test results compared with flying performance in telemetry-tracked aircraft. *Aviatation, Space, and Environ Medicine, 54*(10), 906–911.

Kruk, R., & Regan, D. (1996). Collision avoidance: A helicopter simulator study. *Aviatation, Space, and Environ Medicine, 67*(2), 111–114.

Kruk, R., Regan, D., Beverley, K. I., & Longridge, T. (1981). Correlations between visual test results and flying performance on the advanced simulator for pilot training (ASPT). *Aviatation Space and Environ Medicine, 52*(8), 455–460.

Lee, D. N. (1976). A theory of visual control of braking based on information about time-to-collision. *Perception, 5*, 427–459.

Levitt, H. (1971). Transformed up–down methods in psychoacoustics. *Journal of the Acoustical Society of America, 49*, 65–69.

Montagne, G., Laurent, M., Durey, A., & Bootsma, R. (1999). Movement reversals in ball catching. *Experimental Brain Research, 129*, 87–92.

NHSTA (National Highway Traffic Safety Administration) (1966). Traffic safety facts, Washington, DC.

Peper, L., Bootsma, R. J., Mestre, D. R., & Bakker, F. C. (1994). Catching balls: How to get the hand to the right place at the right time. *Journal of Experimental Psychology: Human Perception and Performance, 20*(3), 591–612.

Portfors-Yeomans, C. V., & Regan, D. (1996). Cyclopean discrimination thresholds for the direction and speed of motion in depth. *Vision Research, 36*(20), 3265–3279.

Portfors-Yeomans, C. V., & Regan, D. (1997). Discrimination of the direction and speed of motion in depth of a monocularly visible target from binocular information alone. *Journal of Experimental Psychology: Human Perception and Performance, 23*(1), 227–243.

Regan, D. (1986). Visual processing of four kinds of relative motion. *Vision Research, 26*, 127–145.

Regan, D. (1992). Visual judgments and misjudgments in cricket and the art of flight. *Perception, 21*, 91–115.

Regan, D. (1993). Binocular correlates of the direction of motion in depth. *Vision Research, 33*(16), 2359–2360.

Regan, D., & Beverley, K. I. (1973). Some dynamic features of depth perception. *Vision Research, 13*, 2369–2379.

Regan, D., & Beverley, K. I. (1978). Looming detectors in the human visual pathway. *Vision Research, 18*, 415–421.

Regan, D., & Beverley, K. I. (1979). Visually guided locomotion: Psychophysical evidence for a neural mechanism sensitive to flow patterns. *Science, 205*, 311–313.

Regan, D., & Beverley, K. I. (1980). Visual responses to changing size and to sideways motion for different directions of motion in depth: Linearization of visual responses. *Journal of the Optical Society of America, 11*, 1289–1296.

Regan, D., & Beverley, K. I. (1983). Visual fields for frontal plane motion and for changing-size. *Vision Research, 23*, 673–676.

Regan, D., & Gray, R. (2000). Visually guided collision avoidance and collision achievement. *Trends in Cognitive Sciences, 4*(3), 99–107.

Regan, D., & Gray, R. (2004). A step-by-step approach to research on time to contact and time to passage. In H. Hecht & G. J. P. Savelsbergh (Eds.), *Theories of time-to contact*. *Advances in Psychology* 135 (pp. 173–228). Amsterdam: Elsevier.

Regan, D., & Hamstra, S. J. (1993). Dissociation of discrimination thresholds for time to contact and for rate of angular expansion. *Vision Research, 33*, 447–462.

Regan, D., & Kaushal, S. (1994). Monocular discrimination of the direction of motion in depth. *Vision Research, 34*(2), 163–177.

Regan, D., & Vincent, A. (1995). Visual processing of looming and time to contact throughout the visual field. *Vision Research, 35*, 1845–1857.

Regan, D., Beverley, K. I., & Cynader, M. (1978). Stereoscopic depth channels for position and for motion. In S. J. Cool & E. L. Smith (Eds.), *Frontiers of visual science* (pp. 351–372). New York: Springer.

Regan, D., Beverley, K. I., & Cynader, M. (1979). The visual perception of motion in depth. *Scientific American, 241*, 136–142.

Regan, D., Erkelens, C. J., & Collewijn, H. (1986a). Necessary conditions for the perception of motion in depth. *Invest Ophthalmology and Visual Science, 27*, 584–587.

Regan, D., Erkelens, C. J., & Collewijn, H. (1986b). Visual field defects for vergence eye movements and for stereomotion perception. *Invest Ophthalmology and Visual Science, 27*, 806–819.

Regan, D., Gray, R., Portfors, C. V., Hamstra, S. J., Vincent, A., Hong, X. H., Kohly, R., & Beverley, K. I. (1998). Catching, hitting and collision avoidance. In L. Harris & M. Jenkin (Eds.), *Vision and action* (pp. 171–209). New York: Cambridge University Press.

Richards, W., & Regan, D. (1973). A stereo field map with implications for disparity processing. *Investigative Ophthalmology, 12*, 904–909.

Tresilian, J. R., & Lonergan, A. (2002). Intercepting a moving target: Effects of temporal precision constraints and movement amplitude. *Experimental Brain Research, 142*(2), 193–207.

Tyler, C. W. (1975). Characteristics of stereomovement suppression. *Perception and Psychophysics, 17*, 225–230.

Welchman, A. E., Tuck, V. L., & Harris, J. M. (2004). Human observers are biased in judging the angular approach of a projectile. *Vision Research, 44*(17), 2027–2042.

Williams, A. M., Davids, K., & Williams, J. G. (1999). *Visual perception and action in sport*. London: E and FN Spon.