



## Extra-retinal signals support the estimation of 3D motion

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### ABSTRACT

In natural settings, our eyes tend to track approaching objects. To estimate motion, the brain should thus take account of eye movements, perhaps using retinal cues (retinal slip of static objects) or extra-retinal signals (motor commands). Previous work suggests that extra-retinal ocular vergence signals do not support the perceptual judgments. Here, we re-evaluate this conclusion, studying motion judgments based on retinal slip and extra-retinal signals. We find that (1) each cue can be sufficient, and, (2) retinal and extra-retinal signals are combined, when estimating motion-in-depth. This challenges the accepted view that observers are essentially blind to eye vergence changes.

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### 1. Introduction

How do we estimate the motion of an approaching object? If the eyes are stationary (Fig. 1A) the retinal position of the object will change differentially on the two retinæ, and the brain could use this change in absolute retinal disparity to detect the motion. However, an observer will normally try to track a moving object, thus minimizing absolute retinal disparities. If so, the observer could use extra-retinal cues about pursuit eye movements to judge the object's motion (Fig. 1B). This idea has a long history (Helmholtz, 1910; Sherrington, 1918), but whilst extra-retinal cues to horizontal version (eyes moving in the same direction) are accepted to play a role in lateral motion perception (Brenner, 1991; Freeman & Banks, 1998; Turano & Massof, 2001), previous studies have suggested that extra-retinal cues to horizontal vergence (eyes moving in opposite directions) provide very poor information about objects moving in depth (Erkelens & Collewijn, 1985b; Regan, Erkelens, & Collewijn, 1986). The latter studies reported that tracking a large moving object does not lead to a perception of motion-in-depth unless other static structures are visible. This suggests that changing vergence information is not provided by extra-retinal cues, but rather by the retinal slip of static structures (Fig. 1D).

To isolate binocular information, Erkelens and Collewijn (1985b) employed stimuli that changed in disparity but had constant retinal size. This is potentially problematic because it can result in a strong conflict between binocular cues and retinal size (looming) cues to motion-in-depth – specifically, binocular signals

specify motion whilst retinal size cues specify no movement of the object. An indication that this might be critical is that some motion-in-depth can be perceived without static references if large targets are replaced by small ones (Regan et al., 1986; Brenner, Van Den Berg, & Van Damme, 1996; Harris, 2006). This suggests that extra-retinal cues can be useful when cue conflict is less evident. Thus, the extra-retinal contribution to the estimation of motion-in-depth may need to be re-evaluated.

Here we test whether observers can discriminate motion-in-depth based on extra-retinal cues. In Experiment 1, we measured this ability by comparing motion direction discrimination thresholds when the eyes were already moving at target motion onset (extra-retinal cues available) and when they were stationary at motion onset (retinal cues available). Our results suggest that extra-retinal cues can be sufficient to support estimates of motion-in-depth. In Experiment 2 we examined the trial-by-trial relationship between psychophysical judgments and the amount of retinal and extra-retinal information available. We found that psychophysical judgments were best accounted for on the basis that observers combine retinal and extra-retinal signals to judge direction of motion. We conclude that, in contrast to the accepted view, extra-retinal signals can be used to support perceptual judgments of motion-in-depth.

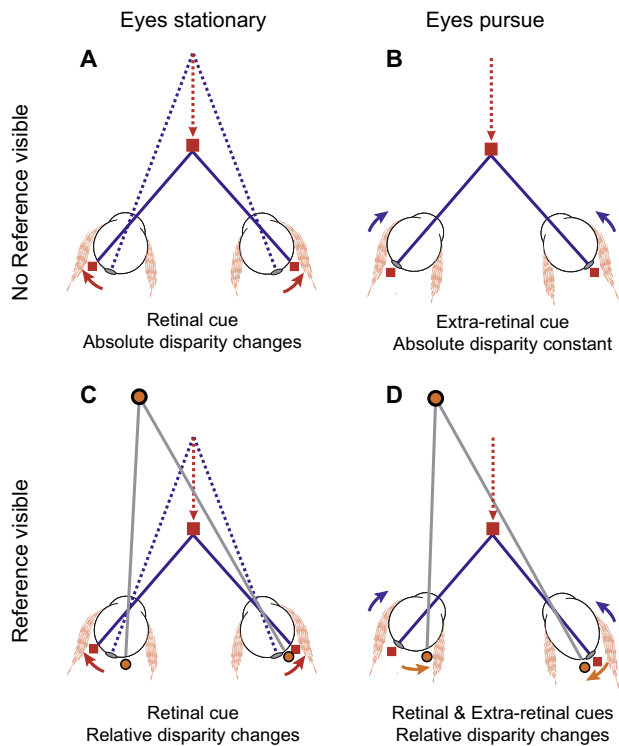
### 2. Experiment 1

#### 2.1. Method

Observers (the authors and 3 naïve participants) sat 80 cm from a 39.2 by 29.3 cm (27.5 × 20.75 deg) computer screen with their

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**Fig. 1.** An illustration of the information available for motion-in-depth estimation. (A) If the eyes are still, target motion produces a retinal motion signal (retinal slip of the square target). (B) This retinal slip signal is reduced as the eyes pursue the target, so that with perfect pursuit (and hence no retinal slip) in the dark, information about eye rotation must derive from extra-retinal sources. (C) The presence of a static reference (circle) provides information about motion-in-depth from the changing relative disparity, irrespective of any eye movements. (D) Moving the eyes in the presence of a static marker also produces retinal slip of the marker that provides information about eye rotation.

chin and head supported. The screen's spatial resolution (815 by 611 pixels) was improved using anti-aliasing techniques. Stereo-images were presented sequentially using shutter spectacles (60 Hz per eye). Experiments were conducted in a totally dark room. Periodic room illumination prevented dark adaptation. Stimuli were drawn with the CRT's red gun as the shutter spectacles have little cross-talk for red images. A red filter in front of the CRT removed residual light from the black screen. Observers pressed one of two buttons on the computer's mouse to indicate whether the target moved towards them or away from them. They were instructed to indicate the direction in which the target moved just before it disappeared. An audible beep provided feedback after correct responses.

Observers were instructed to fixate a small square target ( $6.2 \times 6.2$  arcmin) surrounded by 200 equilateral triangles (with side lengths 0.72 deg). The positions of the triangles in this background stimulus were randomly assigned at the start of each trial, avoiding a 1.43 deg radius around the target. To mask any visible changes in the triangles as they shifted across the screen (such as aliasing effects from the interaction between the triangles and the pixels), each triangle rotated at 120 deg/s about its centre. Half the triangles rotated clockwise, the other half anti-clockwise. Experimental conditions were interleaved and each observer performed 1000 trials. To ensure that observers' judgments were based on binocular information, the retinal size of the target and background stimulus remained constant irrespective of the simulated depth position. Thus there was a conflict between looming and binocular cues to motion-in-depth. This conflict was large for the background, however, since the target was small, the 'missing'

changing size following the removal of the background was not compelling. Had looming been provided after the background was removed, the maximum change in target size would have been an expansion of the target's edges by 1.4 arcmin. We measured thresholds in three conditions:

### 2.1.1. Eyes moving: large-field

To measure performance based on extra-retinal cues, the observers' eyes had to be smoothly pursuing the target (through symmetrical changes in vergence) before performance was measured. Otherwise subjects may base their judgments on the retinal signals that initiate the eye movements. To achieve this, we initially surrounded the target by a large, structured background and varied the simulated depth position of the background and target together over time, without changing retinal size (Fig. 2A: solid line). This large stimulus ( $22 \times 17$  deg) promotes accurate pursuit (Erkelens & Collewijn, 1985a) whilst motion-in-depth should be imperceptible (Erkelens & Collewijn, 1985b; Regan et al., 1986). To make sure that motion-in-depth of the large background was imperceptible we measured observers' discrimination performance when the target disappeared at the same time as the background (Fig. 2A: 0 ms point).

### 2.1.2. Eyes moving: isolated target

If extra-retinal signals can support perceptual estimates, pursuit of the target after removal of the background should allow observers to judge motion direction as the conflict with retinal size information is considerably attenuated. To assess this, we measured performance for three different durations of target motion (100, 200 or 300 ms) after disappearance of the background (Fig. 2A: dashed line).

### 2.1.3. Eyes-stationary: isolated target

Based on previous measurements of eye pursuit (Erkelens & Collewijn, 1985a), it is expected that the large background would provide a good target for pursuit. Nevertheless, it was unlikely that observers would track a target moving in depth perfectly. If the pursuit gain was less than one, some retinal slip would be present in conditions designed to isolate extra-retinal signals. We therefore, measured performance when retinal slip was the only cue available to observers. We used the stimulus described above, with the exception that neither target nor background moved in depth prior to the disappearance of the background (Fig. 2B). Thus the eyes should be stationary at the onset of isolated target motion and target motion will deliver primarily retinal motion signals.

We measured direction discrimination thresholds ("towards" vs. "away") by varying the target's speed using a 2-up, 1-down staircase. The speed was halved after every correct response, and quadrupled after every error. Detection thresholds (67% correct) for each condition were estimated by averaging the logarithms of the target's speed at the reversal points in the staircase. The first four reversals in each staircase were excluded from the analysis. The 5th reversal was also excluded in staircases with uneven numbers of reversals. We included a ceiling value for the staircase to prevent the stimuli exceeding the limits for binocular fusion. This ceiling value was the initial simulated motion-in-depth speed of 50.4 cm/s (around 2.2 deg/s for receding targets and 4.2 deg/s for approaching targets; exact values depend on the subject's inter-pupillary distance). Observers' performance was evaluated by comparing their thresholds in each condition and duration with a bootstrapped distribution of values expected by chance. Such a distribution for chance performance exists because the ceiling value imposed on the staircase procedure ensured that random responses would not increase target speed beyond the upper bound of 50.4 cm/s.

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