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# Strong percepts of motion through depth without strong percepts of position in depth

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Encoding the motion of objects through three spatial dimensions is a fundamental challenge for the visual system. Two binocular cues could contribute to the perception of motion through depth: changes in horizontal disparity (CD) and interocular velocity differences (IOVD). Although conceptually distinct, both cues are typically present when real objects move. Direct experimental isolation of the putative IOVD cue has remained elusive, and it is therefore unclear to what extent the visual system relies on it. We have found that binocularly anticorrelated stimuli impair position in depth judgments, but motion through depth judgments for the same stimuli are relatively unaffected. This dissociation of direction of motion from position in depth provides strong evidence that percepts of motion through depth are not based exclusively on estimating changes in disparity. Horizontal IOVDs appear to complement the CD cue. Vertical IOVDs fail to yield comparable performance, further implicating a comparison of horizontal interocular velocity and also ruling out explanations of our results based on monocular cues. These results suggest that (1) IOVDs are a robust cue to motion through depth; (2) IOVDs and retinal disparities exhibit similar horizontal/vertical anisotropies, consistent with the geometry of binocular viewing; and (3) binocular anticorrelation provides means to titrate the relative contributions of CD and IOVD cues.

Keywords: motion, depth, disparity, stereomotion, anticorrelation

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# Introduction

Despite large literatures on the neural processing of both visual motion and static depth, relatively little is known about how binocular information is used to estimate the direction of objects moving through depth. Neurophysiological experiments have not yet fully characterized how visual cortex encodes the direction of motion through depth (Akase, Inokawa, & Toyama, 1998; Brooks & Mather, 2000; Cynader & Regan, 1982; DeAngelis & Newsome, 2004; Maunsell & Van Essen, 1983; Poggio & Talbot, 1981; Regan & Cynader, 1982; Toyama, Komatsu, Kasai, Fujii, & Umetani, 1985; Zeki, 1974). We therefore performed a series of psychophysical

experiments to characterize the binocular cues used to compute motion through depth.

Binocular disparity is a critical cue for the perception of static position in depth (Wheatstone, 1838). One possibility is that the visual system monitors changes in disparity (CD) to compute motion through depth. Prior work on the perception of static position in depth has employed binocularly anticorrelated random dot displays in which corresponding points in the two eyes have opposite contrast polarity: A dark dot in one eye is paired with a light dot in the other eye. Such displays have been shown to yield weak, distorted, or nonexistent percepts of depth (Cogan, Kontsevich, Lomakin, Halpern, & Blake, 1995; Cumming & Parker, 1994, 1997; Neri, Parker, & Blakemore, 1999; Pope, Edwards, & Schor, 1999). If the

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perception of motion through depth depended solely on estimating the change of depth signals over time, one would expect that perception of motion through depth would be correspondingly impaired by anticorrelation.

However, the visual system might use a second cue, interocular velocity differences (IOVD), to detect motion through depth (Beverley & Regan, 1973). Although the CD and the IOVD cues normally occur in concert, IOVDs are logically distinct and can be estimated without regard to disparity. An IOVD mechanism could encode motion through depth by comparing corresponding monocular velocities in the two eyes. Experimental stimuli have isolated the CD cue and have demonstrated that it is sufficient for the perception of motion through depth (Cumming & Parker, 1994; Harris & Watamaniuk, 1995). Likewise, stereomotion thresholds are well-correlated with stereo discrimination thresholds, but not with frontoparallel motion thresholds (Cumming, 1995). Later work, however, has suggested a contribution of the IOVD cue; percepts of motion through depth are affected by the presence or absence of IOVDs, as well by monocular adaptation (for references, see Conclusions section).

We sought to test whether the visual system can compute motion through depth from moving stimuli when disparity signals are degraded by binocular anticorrelation. Robustness of motion in depth percepts to anticorrelation would support the notion that the visual system relies on the IOVD cue under such conditions.

We found that the perception of motion through depth is largely unaffected by binocular anticorrelation, even when percepts of position in depth are greatly impaired for the same stimuli. Our results demonstrate that IOVDs are a distinct and robust cue to motion through depth and suggest that binocular anticorrelation is a useful tool for distinguishing the contributions of changing disparities and interocular velocities.

# **General methods**

In three psychophysical experiments, observers viewed stereoscopic dynamic random dot displays that contained either lateral motion (LM) or motion through depth (MTD) and made judgments regarding *position* in depth or *direction* of motion. Lateral motion can be changed to motion through depth by reversing the sign of the velocity in one eye's image. When an object has the same velocity in the two eyes, and thus has constant disparity, it is perceived to be moving laterally without any change in depth. When the direction of motion is reversed in one eye, the object is perceived as moving directly towards (or away from) the observer without any lateral motion. We emphasize that a dramatic perceptual change can be made with a small stimulus change (the sign of velocity) that otherwise preserves all of the important monocular visual parameters.

#### **Observers and apparatus**

Four experienced psychophysical observers (the authors and one naive observer) participated in all experiments. All human subject procedures were approved by the Institutional Review Board at The University of Texas at Austin.

Stimuli were presented on a linearized  $30.5 \times 23$  cm  $(15.5 \times 11.8 \text{ deg of visual angle}) 60 \text{ Hz LCD display}$ (mean luminance =  $4.7 \text{ cd/m}^2$ ). Viewing distance was 110 cm. Experiments were conducted in a mock MRI scanner (for comparison with ongoing imaging studies). Observers lay supine and viewed stimuli at the anterior end of the bore through a mirror stereoscope. A septum ensured that the left and right half images could be seen only by the left and right eyes, respectively. Prior to each run, the observer adjusted the mirrors of the stereoscope to achieve binocular fusion of a central fixation point. This geometry introduced a small relative rotation of the monocular half images in the image plane. We corrected this rotation in software: The observer adjusted the relative rotation of test half-images until the entire binocular image was comfortably fused. The fixation point contained nonius lines that the observer could use to monitor vergence throughout the experiment.

### General stimuli and tasks

In this section, we first describe the binocular 3D percepts generated by our visual stimuli to help the reader understand the tasks more clearly and intuitively. The



Figure 1. Schematic of the visual display and percept. Observers viewed left and right halves of the visual display with the left and right eye, respectively, yielding a 3D percept of two volumes (one closer than fixation, one further) containing columns of dots moving in opposite directions. Observers judged dot position in depth (Experiment 1A) or direction of motion (Experiment 1B).

monocular details of the underlying 2D visual displays are then given in the next section. The bottom of Figure 1 illustrates the layout of our visual displays. Each monocular half image (and thus the binocular percept) consisted of two columns of dots, placed horizontally on either side of fixation. The dots, half of which were black and half of which were white, were displayed against an intermediate gray background. On each trial, each binocular column of dots appeared to be within one of four volumes, two of which are depicted at the top of Figure 1. If the right volume of dots appeared nearer than fixation, the left volume appeared further away, or vice versa. In other words, the volumes were always diagonally juxtaposed on the x-z plane.

For the motion through depth (MTD) stimulus, the dots moved towards the observer in the right volume and away in the left volume, or vice versa. For the lateral motion (LM) stimulus, the dots moved to the right in the right volume and to the left in the left volume, or vice versa. Thus, the dots always moved in opposite directions in the two diagonally opposed volumes. On any given trial, then, an observer could either make a judgment about the direction of motion of the dots *within* the volumes (direction judgment), or about the relative locations *of* the volumes (position in depth judgment).

The position of the volume (near/far) and the direction of the motion within the volume (towards/away or rightward/leftward) were independently and randomly chosen on each trial. In all experiments, the probability of the right (or left) volume being near (or far) was 50/50, as was the probability of the right (or left) volume containing motion towards (or away) for the MTD stimulus and leftwards (or rightwards) for the LM stimulus. In all results reported, the data were averaged across these variables to yield the proportion of correct responses for each experimental condition.

In all experiments, each trial consisted of a 1-sec stimulus presentation. Key press responses initiated the next trial. No feedback was given. We measured the proportion of correct responses for each condition. Dependencies of the proportion of correct responses on the parametric variation of the experimental conditions were well fit by linear psychometric functions. All statistics were bootstrapped by (1) resampling the original data 1000 times with replacement; (2) fitting each resampled data set with a linear psychometric function; and (3) calculating a confidence interval from the resulting distribution of the relevant aspect (e.g., slope or endpoint) of the 1000 psychometric function fits.

#### Stimulus details

In all experiments, subjects stereoscopically viewed random dot displays. The 16 dots in each monocular halfimage were 0.15 deg in diameter. Each was assigned an initial random location in one of two volumes (described above), with the constraint that there was at least 0.75 deg of separation between adjacent dots. Eight of the dots in each half image were white and the remaining eight were black. All dots had the same speeds, durations, and range of disparities. Dots were antialiased to obtain subpixel position accuracy.

The two volumes containing the dots were 15 deg in height. Horizontal eccentricity of the volumes spanned from 1.5 to 2 deg (Experiments 1 and 3) or from 1 to 7 deg (Experiment 2). Disparities ranged from 0 to 12 arcmin crossed for the near volume and from 0 to 12 arcmin uncrossed for the far volume. Each dot traveled a horizontal extent of 0.2 deg at either 0.4 deg/sec (Experiments 1 and 3) or 0.2 deg/sec (Experiment 2). Because each dot started a trial at a randomly chosen disparity in its containing volume, it would usually "wrap" once (Experiment 2) or twice (Experiments 1) and 3) during each stimulus presentation. These sparse, well-separated dot displays provided relatively unambiguous binocular matches, a feature that becomes important when considering our main experimental manipulation, described below.

### Manipulation of interocular correspondence

Our primary stimulus manipulation of interest was the interocular correspondence (IC), the degree to which the contrast polarity of dots in the two stereoscopic halfimages matched one another. To manipulate IC, we changed the luminance of the appropriate number of randomly selected dots in one half image from white to black or vice versa. We varied IC from 100% (each white dot in one half image had a white counterpart in the other half image, and each black dot in one half image was paired with a black counterpart in the other half image) to 0% (each white dot in one half image was paired with a black dot in the other and vice versa). Thus, in a 100% IC stimulus, every dot in one eye was paired with a dot of the same contrast polarity in the other eye; for a 50% IC stimulus, half of the dots were paired with dots of the same polarity and the other half were paired with dots of the opposite polarity; for a 0% IC stimulus, every dot was paired with a dot of opposite polarity. Thus, every dot in one half-image was always paired with a corresponding dot in the other half image, and the only manipulation was the relative proportion of dots having same or opposite contrast polarities between two eyes.

Movies 1A and 1B contain illustrations of the 100% and 0% IC motion through depth (MTD) conditions, respectively. The movies require free fusing. To make for an effective demonstration, the movies differ from the stimuli used in the experiments in two ways. Dots have reduced speed and move from crossed to uncrossed disparities (or vice versa): this way dots do not have to wrap as the result of moving past the boundary of their confining volume, which introduces apparent-motion noise. In our actual



Movie 1. Movies illustrating the visual display. The movies require free fusing. (A) Motion through depth (MTD) stimulus at 100% IC. After fusing the dots should appear to lie outside the plane of fixation in the static image. (B) Motion through depth (MTD) stimulus at 0% IC. After fusing, position of dots in depth should be difficult to perceive in the static image due to the dots having opposite contrast in the two eyes. Despite the clear differences between panels A and B in the percepts of position in depth, both movies yield clear percepts of motion through depth when animated.

experimental stimuli, the dots wrapped to remove the confounding cue of a change in average disparity over the course of a trial. As we will show in our psychophysical results, the *direction* of motion can be perceived in both the 100% and the 0% IC conditions. In contrast, perceived *position* in depth is impaired in the 0% IC condition, which can be verified by pausing the movie midway through the animation.

Interocular *correlation* is typically used to describe dense random element stereograms (Cormack, Stevenson, & Schor, 1991; Julesz & Tyler, 1976; Tyler & Julesz, 1978). However, our dot displays were intentionally sparse (see Figure 1) to minimize the contributions of potential false matches (Neri et al., 1999), allowing our experiments to focus exclusively on the effects of binocular anticorrelation for unambiguously matched elements. We therefore suggest it is more intuitive to think in terms of the percentage of dots having contrast polarity *correspondence* in the two half-images.

We performed several pilot experiments to explore stimulus parameter ranges and noted that the main results we report were robust to moderate changes in the particular parameter values and stimulus geometry used. In particular, we presented low density dot patterns in columns to reduce the number of false horizontal matches between dots and to allow for a simple psychophysical task common to all conditions. However, at least qualitatively similar percepts arise with full-field, relatively dense dot displays. Likewise, we used relatively slow monocular velocities to limit the number of times dots left the visible aperture (and re-appeared on the other side), but similar percepts were experienced using faster velocities. Finally, we note that the contrast and (monocular) velocity of the stimuli were clearly suprathreshold so that stimulus visibility and/or detectability per se were never limiting factors. Instead, accuracy was affected by manipulations of interocular correspondence and often spanned the parathreshold range with respect to this main variable of interest.

# **Experiment 1**

## Perception of position in depth is impaired by binocular anticorrelation, but perception of motion through depth is unaffected

Our first experiment was designed to compare discrimination accuracy for judgments of motion through depth and position in depth. If the perception of motion through depth depends solely on monitoring changes in disparity, accuracy levels for position in depth (which was necessarily based only on disparity in our displays) should serve as an upper bound for the accuracy of motion through depth judgments on the same stimulus. On the other hand, if accuracy for motion in depth judgments exceeds accuracy for position in depth judgments, we can infer the contribution of another cue. To test this, we varied the interocular correspondence of the left and the right eye's images from 100% IC (perfectly correlated) to 0% IC (completely anticorrelated) and measured the dependence of motion through depth and position in depth judgments on the same stimuli.

#### Methods

The first experiment consisted of two tasks segregated into alternating experimental runs (Experiments 1A and 1B). The only difference between these experiments was the task; the stimuli were identical. In Experiment 1A, observers performed a *position* in depth judgment, indicating whether the right volume was nearer or farther than the left volume. In Experiment 1B, observers performed a *direction* of motion judgment that could be conceptualized as follows: Observers considered the dots in the two volumes to roughly define the surface of a single vertical cylinder and judged the direction of rotation of this cylinder. Effectively, when the observer saw an MTD stimulus, the observer judged whether dots in the right (left) volume were moving towards (away). When the observer saw an LM stimulus, they judged whether dots in the nearer (farther) volume were moving leftward (rightward). Observers reported that by conceptualizing this as a rotation task, they could perform the same sort of judgment in the two conditions. This was merely a convenient way of thinking about the task; the important point is that subjects discriminated the relative directions of motion of the two volumes, regardless of the experimental condition (LM or MTD). Note that, as mentioned above, the only difference between the MTD stimulus and the LM stimulus was the reversal of the velocity in one eye's half-image.



Figure 2. Results from Experiment 1. (A) Accuracy as a function of interocular correspondence (IC) for position in depth task (Experiment 1A). Accuracy decreased with decreased IC for both types of dot motion (gray circles, motion through depth [MTD]; black circles; lateral motion [LM]). Each column shows data from a different observer. (B) Accuracy for direction of motion task (Experiment 1B). Accuracy in the LM condition dropped with IC (black circles), similar to the data in Experiment 1A. But accuracy was unimpaired for the MTD condition (gray circles). (C) Psychometric function slopes from Experiments 1A and 1B. All judgments that depend on the perceived dot position yielded negative slopes, indicating a decrease in performance with decreasing IC. Only slopes from the MTD condition of Experiment 1B are near zero, confirming that perceived motion through depth is robust to anticorrelation, and exceeds judgments of position in depth for the same stimuli. Points show slope fit to each psychometric function from Figures 2A and 2B (corresponding color-coding); error bars show bootstrapped 95% confidence intervals.

#### Results and discussion

In Experiment 1A, we measured accuracy in a near/far position in depth judgment task as we manipulated the degree of IC in random dot displays. As shown in Figure 2A, accuracy was at its highest at 100% IC for all observers but fell off markedly with decreasing IC. An IC of 0 (which corresponds to complete anticorrelation) greatly impaired observers' ability to discriminate which volume of dots was in front of or behind the plane of fixation. This effect was similar for both lateral motion and motion through depth displays (Figure 2A). This sizable impairment of depth discrimination for anticorrelated displays replicates previous findings using static displays.

In Experiment 1B, we measured accuracy in a direction of motion judgment on the same stimuli. For lateral motion, observers exhibited a decline in performance with decreasing IC similar to that observed in Experiment 1A (Figure 2B, black circles). This is not surprising, given that the ability to judge whether the near or far dots were moving rightward should be limited by the ability to judge simply which dots were near and which were far.

In striking contrast, the gray circles in Figure 2B show that the accuracy of direction judgments in motion through depth (MTD) was largely unaffected by reduced IC. This is evident in the relatively flat psychometric functions for all observers.

To illustrate this point further, Figure 2C depicts the estimated slope of the linear fits to the data in Figures 2A and 2B. The open gray circles cluster around 0, indicating no effect of IC on MTD judgments, whereas the estimated slopes in all other conditions are negative, indicating a decrease in proportion correct responses with decreased IC. Thus, the robustness of motion through depth to IC contrasts strongly with all other experimental results, including the accuracy of the position in depth judgments performed on the same stimuli. Even when observers could not perceive dot position, they were able to judge whether those same dots were moving towards or away from them. Consistent with this psychophysical dissociation, observers qualitatively reported that they could easily see the direction of motion in anticorrelated displays (Movie 1B) but that they could not perceive the position of the same dots in depth.

This result implies that motion through depth is not processed simply by monitoring changes in disparity signals over time. It is difficult to explain our observation based on exclusive reliance on changing disparity because judgments of position in depth are impaired by anticorrelation, but judgments of the direction of motion through depth are not. In other words, the disparity signals that supported position in depth judgments (Experiment 1A) are insufficient to account for the accuracy of the direction of motion in depth judgments (Experiment 1B). This dissociation implicates IOVDs as an additional source of information.

# Experiment 2

# Perception of motion through depth in the absence of the interocular velocity (IOVD) cue is not robust to anticorrelation

In Experiment 2, we further investigated the effects of interocular correspondence on a stimulus that contained the CD cue but not the IOVD cue. The results of Experiment 1 demonstrated that binocular anticorrelation impaired percepts of position in depth. We reasoned that if this falloff in performance was due to a degradation of the disparity signals used to compute the CD cue, observers should not be able to perceive motion in depth in anticorrelated displays that contain only the CD cue.

Observers viewed a dynamic random dot stereogram that contained the CD cue but not the IOVD cue, as described in the next section. As in Experiment 1B, we varied interocular correspondence from trial to trial and tested whether observers could perform the direction discrimination task.

#### Methods

The observer's task in this experiment was the same as it was for the MTD trials in Experiment 1B: judging the direction of motion of the two sides of the display as leftaway and right-towards or vice versa. In this experiment, we removed the IOVD cue by removing any coherent monocular motion signal from the stimulus. On each screen refresh, each dot was assigned a random spatial position within one of two frontoparallel depth planes (on either side of fixation) that were 15 deg high and extended from 1 to 7 deg in horizontal eccentricity (Figure 3A). These planes swept smoothly in disparity towards or away from the observer at 24 arcmin/sec. All dots were replotted in random positions within each plane on every frame. This removed any coherent global motion signals in either half image, so no systematic interocular velocity differences were present. This allowed us to test the effects of interocular correspondence on the CD cue in isolation.

We emphasize that it is not geometrically possible to remove IOVDs from the stimulus used in Experiment 1 without changing other characteristics of the display. Removing IOVDs will necessarily change the spatiotemporal spectrum of the stimulus. We therefore focused on designing a stimulus that (1) contained CD cues, while A Experiment 2



Figure 3. Stimulus and results from Experiment 2. (A) Stimulus schematic. Two disparity-defined planes of dots, diagonally opposite from fixation, moved in opposite directions. Each dot was replotted in a random position in its plane with each screen refresh, so that no consistent IOVD signal was present. (B) Accuracy as a function of interocular correspondence. Accuracy was well above chance for stimuli with high degrees of IC but was reduced to chance (50%) for anticorrelated stimuli. Each set of points and corresponding line indicates data from a different subject. Bootstrapped 95% confidence intervals for the psychometric function (proportion correct) at IC = 0% were: AH (0.46, 0.55), LC (0.43, 0.52), BR (0.44, 0.54), TC (0.40, 0.50).

eliminating all IOVD cues, and (2) supported percepts of MTD at 100% IC (perfectly correlated). If anticorrelation impairs MTD percepts for this stimulus, one can infer that the IOVD cues that we removed from it supported the robustness of the results reported in Experiment 1.

Similar to Experiment 1, each half image contained 8 dots on either side of fixation. The planes began at a random disparity within their respective volume and were wrapped in depth when they reached the limit of the volume during a trial. The observers were instructed to judge the slow, smooth change in depth and ignore the jump (which was relatively easy).

Each observer ran 3 sessions of 400 trials each, corresponding to 240 total trials at each of the 5 levels of IC.

#### Results and discussion

Figure 3B shows that observers were able to judge the direction of motion through depth at 100% IC. But accuracy decreased with decreasing IC, falling to chance levels for 0% IC (anticorrelated) displays. The CD cue alone could not support percepts of motion through depth for anticorrelated displays (rightmost data points), even when it could for fully correlated displays (leftmost data points).

These results show no robustness to IC, contrasting with the results in Experiment 1B in which decreasing IC did not degrade accuracy. In Experiment 1B, observers performed the same basic MTD task, but the stimuli contained IOVD cues. We therefore conclude that IOVDs play a distinct role in supporting percepts of MTD. IOVDs appear to work in concert with the CD cue, giving motion through depth percepts robustness to binocular contrast mismatches.

We next performed an experiment to verify that IOVD is a binocular cue, distinct from other motion-based cues to depth such as optic flow.

# **Experiment 3**

# Perception of motion through depth is supported by the horizontal component of IOVD

Experiments 1 and 2 suggested that interocular velocity differences play a distinct and important role in the perception of motion through depth. In Experiment 3, we again used anticorrelated displays to emphasize the contribution of the IOVD cue, but this time varied the stimulus orientation between horizontal and vertical. We reasoned that if the IOVD cue is binocular, the strength of this cue should diminish as the display is rotated from horizontal to vertical, consistent with the geometry of binocular viewing. If on the other hand the results of Experiments 1 and 2 were due to monocular or utrocular cues, performance should not be affected by orientation.

#### Methods

Stimuli for this experiment were the same as those for the MTD trials of Experiment 1, except for two details. First, all trials contained 0% IC, which putatively isolated the IOVD cue, or at least severely reduced the contribution of the CD cue. Second, stimulus orientation was set to 0, 30, 60, or 90 deg. Thus, the IOVD cue could either be purely A Experiment 3



Figure 4. Stimulus and results from Experiment 3. (A) Stimulus schematic. Stimuli were identical to those described in Experiment 1, except always had 0% IC, and were rotated 0, 30, 60, or 90 degrees from horizontal. (B) Accuracy as a function of the fraction of horizontal motion in the stimuli. Performance is reduced from near perfect for pure horizontal motion to near chance for pure vertical motion, suggesting that the IOVD cue is specialized for horizontal velocities. Each set of points and corresponding line indicate data from a different subject. Bootstrapped 95% confidence intervals for the psychometric function (proportion correct) at 90 deg rotation (vertical) were AH (0.39, 0.50), LC (0.40, 0.52), BR (0.50, 0.61), and TC (0.49, 0.61).

horizontal (0 deg), purely vertical (90 deg), or a mixture of horizontal and vertical components (see Figure 4A). As in Experiment 1B, observers judged the direction of motion of the dots.

Each observer completed 3 sessions of 320 trials each, corresponding to 240 total trials at each of the 4 orientations.

#### Results and discussion

Figure 4B shows that accuracy in the direction task was strongly dependent upon IOVD orientation, falling from

nearly perfect at 0 deg (horizontal) to chance at 90 deg (vertical). This demonstrates that horizontal IOVDs preferentially contribute to the perception of motion through depth.

This result also precludes the possibility that the observers were using any sort of dichoptic stimulus artifact combined with eye of origin information to help perform the task. If decisions in the prior experiments had been driven simply by monocular signals, we would not expect the orientation of the monocular motion vectors to have any effect on accuracy.

# Conclusions

Our results provide strong support to the idea that horizontal interocular velocity differences are used by the human visual system to compute motion through depth. Although changes in disparity are commonly considered to be the primary cue for motion through depth (Cumming, 1995), our results demonstrate that IOVDs provide a distinct cue that remains useful even when disparity signals are degraded.

Our work extends previous attempts to distinguish the CD and IOVD cues. Several studies have compared stereomotion speed thresholds for dynamic random dot stimuli that contain both CD and IOVD cues to those that contain only CD cues. Although initial studies suggested no additional contribution of the IOVD cue (Cumming & Parker, 1994), more recent work has suggested an effect of IOVD presence (Brooks & Stone, 2006). However, this approach requires comparison of thresholds across different stimuli. Likewise, other threshold studies have shown stereomotion thresholds to be better correlated with static depth thresholds than with frontoparallel motion thresholds (Cumming, 1995).

Monocular motion adaptation has also been shown to affect stereomotion perception, implying the existence of a velocity-based cue (Brooks, 2002b; Fernandez & Farell, 2006; Shioiri, Kakehi, Tashiro, & Yaguchi, 2003). Likewise, additional attempts to isolate the IOVD mechanism have involved simultaneously presenting dissimilar images to the two eyes (Brooks, 2002a; Shioiri, Saisho, & Yaguchi, 2000). However, these approaches require careful consideration of the disparity signals present due to false matches when disparate images are shown to the two eyes.

We propose that the manipulation of interocular correspondence is a useful tool that complements and strengthens the inferences from prior approaches that relied on threshold comparisons or monocular motion. Varying interocular correspondence straightforwardly allows for the psychophysical assessment of the strength of disparity signals, allowing direct comparisons of accuracy levels for the same stimulus. Furthermore, the anticorrelated dots in our sparse displays had unambiguous binocular matches. This further allowed us to characterize the strength of the disparity signals available to support percepts of motion through depth. Anticorrelated stimuli exert known effects on the disparity tuning curves of visual neurons (Cumming & Parker, 1997; Janssen, Vogels, Liu, & Orban, 2003; Krug, Cumming, & Parker, 2004; Ohzawa, DeAngelis, & Freeman, 1990, 1997; Poggio, Gonzalez, & Krause, 1988; Takemura, Inoue, Kawano, Quaia, & Miles, 2001; Tanabe, Umeda, & Fujita, 2004). Future neurophysiological and psychophysical work can manipulate interocular correspondence to parametrically study the CD and the IOVD cues.

Our results support the emerging idea that both CD and IOVD cues are typically used in concert to judge motion through depth. Prior work has suggested that the IOVD cue supplements the CD cue across certain disparities and spatial scales (Brooks & Stone, 2004, 2006), as well as under conditions of monocular occlusion (Brooks & Gillam, 2006). Our results demonstrate that the IOVD cue adds an important degree of robustness to the computation of motion through depth, supporting near perfect performance even when disparity signals (and the corresponding judgments of position in depth) are greatly degraded. More generally, these results suggest that the visual system keeps track of the eye-of-origin associated with velocity signals, distinct from the processing of disparity. How such eye-specific velocity signals are represented in visual cortex remains a topic of ongoing investigation.

Why would the visual system encode a cue that is robust to changes in binocular correlation? Shiny, irregular surfaces often have many loci that reflect vastly different amounts of light to the two eyes (von Helmholtz, 1910). While it may not be critical to precisely estimate position in depth of such an object, it would be advantageous to accurately perceive whether such an object was moving towards or away from one's head.

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# References

- Akase, E., Inokawa, H., & Toyama, K. (1998). Neuronal responsiveness to three-dimensional motion in cat posteromedial lateral suprasylvian cortex. *Experimental Brain Research, 122*, 214–226. [PubMed]
- Beverley, K. I., & Regan, D. (1973). Evidence for the existence of neural mechanisms selectively sensitive to the direction of movement in space. *The Journal of Physiology*, 235, 17–29. [PubMed] [Article]
- Brooks, K. R. (2002a). Interocular velocity difference contributes to stereomotion speed perception. *Journal* of Vision, 2(3):2, 218–231, http://journalofvision.org/ 2/3/2/, doi:10.1167/2.3.2. [PubMed] [Article]
- Brooks, K. R. (2002b). Monocular motion adaptation affects the perceived trajectory of stereomotion. *Journal of Experimental Psychology: Human Perception and Performance, 28,* 1470–1482. [PubMed]
- Brooks, K. R., & Gillam, B. J. (2006). The swinging doors of perception: Stereomotion without binocular matching. *Journal of Vision*, 6(7):2, 685–695, http://journalofvision.org/6/7/2/, doi:10.1167/6.7.2. [PubMed] [Article]
- Brooks, K., & Mather, G. (2000). Perceived speed of motion in depth is reduced in the periphery. *Vision Research*, 40, 3507–3516. [PubMed]
- Brooks, K. R., & Stone, L. S. (2004). Stereomotion speed perception: Contributions from both changing disparity and interocular velocity difference over a range of relative disparities. *Journal of Vision*, 4(12):6, 1061–1079, http://journalofvision.org/4/12/6/, doi:10.1167/4.12.6. [PubMed] [Article]
- Brooks, K. R., & Stone, L. S. (2006). Spatial scale of stereomotion speed processing. *Journal of Vision*, 6(11):9, 1257–1266, http://journalofvision.org/6/11/9/, doi:10.1167/6.11.9. [PubMed] [Article]
- Cogan, A. I., Kontsevich, L. L., Lomakin, A. J., Halpern, D. L., & Blake, R. (1995). Binocular disparity processing with opposite-contrast stimuli. *Perception*, 24, 33–47. [PubMed]
- Cormack, L. K., Stevenson, S. B., & Schor, C. M. (1991). Interocular correlation, luminance contrast and cyclopean processing. *Vision Research*, 31, 2195–2207. [PubMed]
- Cumming, B. G. (1995). The relationship between stereoacuity and stereomotion thresholds. *Perception*, 24, 105–114. [PubMed]
- Cumming, B. G., & Parker, A. J. (1994). Binocular mechanisms for detecting motion-in-depth. *Vision Research*, *34*, 483–495. [PubMed]

- Cumming, B. G., & Parker, A. J. (1997). Responses of primary visual cortical neurons to binocular disparity without depth perception. *Nature*, 389, 280–283. [PubMed]
- Cynader, M., & Regan, D. (1982). Neurons in cat visual cortex tuned to the direction of motion in depth: Effect of positional disparity. *Vision Research*, 22, 967–982. [PubMed]
- DeAngelis, G. C., & Newsome, W. T. (2004). Perceptual "read-out" of conjoined direction and disparity maps in extrastriate area MT. *Public Library of Science Biology*, 2, E77. [PubMed] [Article]
- Fernandez, J. M., & Farell, B. (2006). Motion in depth from interocular velocity differences revealed by differential motion aftereffect. *Vision Research*, 46, 1307–1317. [PubMed] [Article]
- Harris, J. M., & Watamaniuk, S. N. (1995). Speed discrimination of motion-in-depth using binocular cues. *Vision Research*, 35, 885–896. [PubMed]
- Janssen, P., Vogels, R., Liu, Y., & Orban, G. A. (2003). At least at the level of inferior temporal cortex, the stereo correspondence problem is solved. *Neuron*, 37, 693–701. [PubMed] [Article]
- Julesz, B., & Tyler, C. W. (1976). Neurontropy, an entropy-like measure of neural correlation, in binocular fusion and rivalry. *Biological Cybernetics*, 23, 25–32. [PubMed]
- Krug, K., Cumming, B. G., & Parker, A. J. (2004). Comparing perceptual signals of single V5/MT neurons in two binocular depth tasks. *Journal of Neurophysiology*, 92, 1586–1596. [PubMed] [Article]
- Maunsell, J. H., & Van Essen, D. C. (1983). Functional properties of neurons in middle temporal visual area of the macaque monkey: II. Binocular interactions and sensitivity to binocular disparity. *Journal of Neurophysiology*, 49, 1148–1167. [PubMed]
- Neri, P., Parker, A. J., & Blakemore, C. (1999). Probing the human stereoscopic system with reverse correlation. *Nature*, 401, 695–698. [PubMed]
- Ohzawa, I., DeAngelis, G. C., & Freeman, R. D. (1990). Stereoscopic depth discrimination in the visual cortex: Neurons ideally suited as disparity detectors. *Science*, 249, 1037–1041. [PubMed]
- Ohzawa, I., DeAngelis, G. C., & Freeman, R. D. (1997). Encoding of binocular disparity by complex cells in the cat's visual cortex. *Journal of Neurophysiology*, 77, 2879–2909. [PubMed] [Article]
- Poggio, G. F., Gonzalez, F., & Krause, F. (1988). Stereoscopic mechanisms in monkey visual cortex: Binocular correlation and disparity selectivity. *Journal of Neuroscience*, *8*, 4531–4550. [PubMed] [Article]

- Poggio, G. F., & Talbot, W. H. (1981). Mechanisms of static and dynamic stereopsis in foveal cortex of the rhesus monkey. *The Journal of Physiology*, 315, 469–492. [PubMed] [Article]
- Pope, D. R., Edwards, M., & Schor, C. S. (1999). Extraction of depth from opposite-contrast stimuli: Transient system can, sustained system can't. *Vision Research*, 39, 4010–4017. [PubMed]
- Regan, D., & Cynader, M. (1982). Neurons in cat visual cortex tuned to the direction of motion in depth: Effect of stimulus speed. *Investigative Ophthalmology* & Visual Science, 22, 535–550. [PubMed] [Article]
- Shioiri, S., Kakehi, D., Tashiro, T., & Yaguchi, H. (2003). Investigating perception of motion in depth using monocular motion adaptation [Abstract]. *Journal of Vision*, 3(9):856, 856a, http://journalofvision.org/3/9/ 856/, doi:10.1167/3.9.856.
- Shioiri, S., Saisho, H., & Yaguchi, H. (2000). Motion in depth based on inter-ocular velocity differences. *Vision Research*, 40, 2565–2572. [PubMed]
- Takemura, A., Inoue, Y., Kawano, K., Quaia, C., & Miles, F. A. (2001). Single-unit activity in cortical area MST associated with disparity-vergence eye movements: Evidence for population coding. *Journal of Neurophysiology*, 85, 2245–2266. [PubMed] [Article]
- Tanabe, S., Umeda, K., & Fujita, I. (2004). Rejection of false matches for binocular correspondence in macaque visual cortical area V4. *Journal of Neuroscience*, 24, 8170–8180. [PubMed] [Article]
- Toyama, K., Komatsu, Y., Kasai, H., Fujii, K., & Umetani, K. (1985). Responsiveness of Clare–Bishop neurons to visual cues associated with motion of a visual stimulus in three-dimensional space. *Vision Research*, 25, 407–414. [PubMed]
- Tyler, C. W., & Julesz, B. (1978). Binocular crosscorrelation in time and space. *Vision Research*, 18, 101–105. [PubMed]
- von Helmholtz, H. (1910). Die Lehre von den Gesichtswahrnehmungen. In A. Gullstrand, W. Nagel, J. von Kries, & H. von Helmholtz (Eds.), *Handbuch der physiologischen Optik* (vol. 3, 3rd ed.). Hamburg: Voss.
- Wheatstone, C. (1838). On some remarkable, and hitherto unobserved phenomena of binocular vision: Part I. *Transactions of the Royal Society of London, 128,* 371–394.
- Zeki, S. M. (1974). Cells responding to changing image size and disparity in the cortex of the rhesus monkey. *The Journal of Physiology*, 242, 827–841. [PubMed] [Article]