Determinants of the direction illusion: Motion speed and dichoptic presentation interact to reveal systematic individual differences in sign

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When two fields of dots with different directions of movement are presented in tandem, the perceived direction of one is biased by the presence of the other. Although this “direction illusion” typically involves repulsion, with an exaggeration of the perceived angular difference in direction between the dot fields, attraction effects, where the perceived difference is reduced, have also been found under certain presentation conditions. Earlier literature has been inconsistent, and there is debate surrounding the nature of the interactions that facilitate the direction illusion, as well as whether they occur at a local or global stage of the motion processing hierarchy. Here we measured the operating characteristics of the direction illusion by parametrically varying inducer contrast and coherence while examining the effects of stimulus speed and dichoptic presentation. It was found that the magnitude and sign of the direction illusion differed substantially from earlier research. Furthermore, there appeared to be significant interindividual variability, with dichoptic presentation producing an attractive rather than repulsive direction illusion in some participants.

Introduction

The direction illusion

Among the most important features of the visual system is the ability to infer the motion of objects in the external world from their images projected upon the retinas. One phenomenon that has contributed to our understanding of the mechanisms behind motion perception is simultaneous direction repulsion or the direction illusion (DI), where the simultaneous presentation of two sets of motion stimuli with different directions of movement results in the perceived movement direction of one motion component being biased by the presence of the other (Marshak & Sekuler, 1979). Although often referred to as repulsion, as the DI typically involves an enlargement of the perceived angular difference between the two motion directions, repelling the target from the inducer, some attraction effects have also been found, where the perceived direction difference is reduced (Braddick, Wishart, & Curran, 2002; Chen, Meng, Matthews, & Qian, 2005; Grunewald, 2004; Marshak & Sekuler, 1979; Wiese & Wenderoth, 2007). Due to its ability to elicit reliable distortions in perceived direction, the DI has been identified as a useful method for studying the mecha-
nisms behind population coding in motion-selective neuronal populations (Mather & Moulden, 1980).

Research on the DI has relied on two main paradigms: superimposed/transparent and center-surround. Marshak and Sekuler’s (1979) original study utilized superimposed random dot kinematograms (RDKs); two sets of RDKs presented in tandem appear to be moving transparently over each other when the angular difference in their movement directions is sufficiently large, allowing the direction of a single set of dots to be perceptually extracted (Braddick et al., 2002). The transparent arrangement has been employed in the majority of DI studies that followed the original work of Marshak and Sekuler (e.g., Benton & Curran, 2003; Braddick et al., 2002; Chen, Matthews, & Qian, 2001; Curran & Benton, 2003; Dakin & Mareschal, 2000; Farrell-Whelan, Wenderoth, & Brooks, 2012a, 2012b; Grunewald, 2004; Hiris & Blake, 1996; Rauber & Treue, 1999; Wiese & Wenderoth, 2007). In addition to transparent motion, the DI has been investigated using spatially segregated stimuli presenting target and inducer in a concentric center-surround configuration, with the central target set inside a surrounding annulus. Center-surround motion stimuli have included drifting sine-wave gratings (Kim & Wilson, 1997) as well as RDKs (Wiese & Wenderoth, 2010).

Theoretical accounts of the direction illusion

The processing of motion is constrained by the fundamental characteristics of neurons in the visual system; a neuron’s receptive field represents an aperture through which limited and often ambiguous information is derived. In order to overcome this limitation, motion processing is conceptualized as occurring on two levels, with initial extraction of local motion features followed by a global processing stage, where local features are integrated into a broader, global framework (Clifford & Ibbotson, 2002). While neurophysiological and psychophysical research has provided substantial support for this hierarchical view of motion processing (Rubin & Hochstein, 1993; Snowden, 1994), there is some disagreement surrounding whether the DI is primarily the product of local or global interactions (Benton & Curran, 2003; Hiris & Blake, 1996; Kim & Wilson, 1996, 1997).

A generally accepted theory of the DI is the distribution-shift model, which characterizes repulsive interactions as resulting from mutual inhibition between populations of direction-selective neurons (Marshak & Sekuler, 1979; Mather & Moulden, 1980; Rauber & Treue, 1999). The response to a given direction for an appropriately tuned neuron is reduced when a second direction is also presented within the cell’s receptive field. This inhibition is weakest with a wide angular separation between the two directions (Snowden, Treue, Erickson, & Andersen, 1991). The population of neurons tuned to the direction bisecting the two presented directions is inhibited the most, since that population is equally responsive to both directions. At more acute angular separations, mutual inhibition between populations of neurons tuned to the two directions causes a lateral shift in the neuronal response distributions, such that the peaks of the distributions sit above directions with a wider angular separation than those physically present, resulting in an enlarged perceived direction difference (Farrell-Whelan et al., 2012a). Since neurons exhibiting inhibitory interactions have been found at many levels of the visual processing hierarchy, the distribution-shift model leaves open the question of the neural locus of the DI; varying accounts have suggested primary visual cortex (V1) (Hiris & Blake, 1996) or middle temporal area (MT) (Benton & Curran, 2003; Kim & Wilson, 1997).

The distribution-shift model has been challenged however by other theoretical approaches. Dakin and Mareschal (2000) argued that the ability of dot density and speed to affect illusion magnitude was not adequately accounted for by the distribution-shift model. Rather, the illusion could be the product of differential processing of object motion and inferred background motion, the latter being derived from characteristics of the observed stimulus such as target-to-inducer dot ratio and speed. Under this “differential processing model,” spatially coincident motion signals can be attributed not only to the absolute motion of the observed stimuli, but motion relative to a moving background. Accordingly, motion information can be categorized as object-relative (unique to the motion component) or nonobject-relative (common to all motion components). If the nonobject-relative component is underestimated, the relative magnitude of each object-relative component will be correspondingly overestimated, enlarging the perceived absolute direction difference between them. The estimation of these motion components involves a level of spatial integration that is likely to require a global processing locus. Dakin and Mareschal (2000) found that by weighing the relative contributions of the target and inducer to the inferred nonobject-relative motion by their speed and dot density ratio, the magnitude of the direction repulsion was more accurately predicted, suggesting that differential processing may account for the DI.

Further support for the differential processing model was recently provided by Farrell-Whelan et al. (2012a), who found that a static line could produce a shift in the perceived direction of a single set of dots: a “statically-induced direction illusion” reminiscent of the “slalom effect” (Cesàro & Agostini, 1998; Ito & Yang, 2013). A static line with endpoints that are obscured provides no positional reference cues for moving objects along the
axis of its orientation (Farrell-Whelan et al., 2012a). Corresponingly, the static line acts as a reference object for motion stimuli moving orthogonal to the line, but not parallel to it. Consistent with the hypothesis that object-relative motion components (those orthogonal to the line) were weighted more than nonobject-relative components (parallel to the line), a single motion stimulus presented oblique to the line was shifted perceptually towards the perpendicular of the line. Simultaneous direction repulsion was also affected by the presence of a static line. When transparent motion RDKs were presented with a static line orthogonal to the motion stimulus’ nonobject-relative component velocity, the DI was negated. Conversely, a substantial illusion was found when there was no line or when the line was parallel to the nonobject-relative motion component (Farrell-Whelan et al., 2012a).

**Manipulating levels of processing through differential stimulus presentation**

The dichoptic presentation paradigm involves displaying different components of the stimulus (target and inducer) separately to the two eyes to form a combined binocular percept and has been used by a number of researchers to study the DI. The neural locus of perceptual phenomena can be inferred from the change in their magnitude when presented dichoptically. The recombination of dichoptically presented stimuli is generally believed to occur at an intermediate stage of the visual processing hierarchy, as the earliest binocular neurons appear to be located in V1 (Bishop & Pettigrew, 1986). Signals from monoptically presented stimuli, in contrast, do not require recombination and may interact as they pass through exclusively monocular areas such as the retina, lateral geniculate nucleus (LGN) of the thalamus, and monocular regions of V1, in addition to subsequent binocular areas.

Research on the interocular transfer of the DI has yielded mixed results. Kim and Wilson (1997) reported that dichoptic direction repulsion using a center-surround grating stimulus was 80% of its monoptic magnitude, suggesting that the interactions responsible for the DI largely occur after binocular recombination. Similarly, Patterson and Becker (1996) found that the simultaneous presentation of two stereoscopic dot arrays moving in different directions resulted in an enlargement of their perceived directional difference, evidence that repulsive interactions can occur at a binocular level of processing. However, the findings of Kim and Wilson (1997) have been called into question due to the absence of a control measure for baseline effects such as reference repulsion (Rauber & Treue, 1999), and the use of gratings, which possess extraneous orientation information (Wiese & Wenderoth, 2010). Furthermore, other studies have found that dichoptic presentation significantly reduces or even eliminates the effect, indicative of a local, monocular locus of processing. Using a transparent motion stimulus, Grunewald (2004) found that dichoptic direction repulsion was not significantly different to the “baseline” repulsion produced by the binocular presentation of a single set of dots, suggesting that the illusion was absent under dichoptic presentation. However, the presentation of dissimilar images to corresponding areas in the two eyes can result in binocular rivalry, where perception alternates between exclusive dominance of the left and right eye images rather than the two combining to form a single, stable percept (Alais & Blake, 1999). Although the dichoptic presentation of transparent dot stimuli can produce binocular rivalry, negating the DI (Chen et al., 2001), Grunewald (2004) argued that the low dot density he used ensured that rivalry did not occur. This was replicated by Wiese and Wenderoth (2007), who also found that the illusion was completely eliminated when presented dichoptically with a 30° inducing angle but resulted in a small dichoptic attraction effect with a 120° inducer. A subsequent study produced more equivocal results; Wiese and Wenderoth (2010) found, using a center-surround RDK arrangement with which rivalry does not occur, that the illusion exhibited 56% interocular transfer, suggesting a strong monocular component to the DI.

Although dichoptic presentation research has largely found limited interocular transfer of the DI, this low-level locus is difficult to reconcile with psychophysical findings suggestive of global integration. Benton and Curran (2003) found that the DI elicited by a mixed speed inducer RDK was indistinguishable from that produced by a single-speed inducer moving at the same mean speed. Furthermore, the magnitude of the illusion was inconsistent with the predictions of the local processing account, where the differential contribution of each individual speed is aggregated (Benton & Curran, 2003). This suggests that the illusion is caused by globally integrated elements rather than individual components.

**Operating characteristics of the direction illusion**

Despite the ability of dichoptic presentation to restrict which primary afferent pathways carry the stimulus information, the effects of differential presentation conditions on psychophysical phenomena may remain latent at high levels of contrast (Tadin, Blake, & Chong, 2006). Although research on the DI has invariably shown some level of attenuation with dichoptic presentation, single measurements at fixed
signal strength nonetheless provide limited information about how the effect changes under different presentation conditions. By instead measuring operating characteristics of the illusion with stimuli of varying contrast or coherence, it is possible to ascertain not only the degree of signal strength reduction associated with dichoptic presentation, but also whether this reflects a simple shift in the operating characteristic or a transformation suggestive of more complex neural processes (Pearson & Clifford, 2005). Kim and Wilson (1997) took this approach by estimating the tuning curve of a center-surround DI stimulus as contrast was varied. However, their use of sinusoidal gratings represents a potential confound, as the magnitude of the DI with gratings could be magnified or even wholly accounted for by the static tilt illusion (Wiese & Wenderoth, 2010). In addition, they only measured the operating characteristics for binocular viewing, leaving open the question of whether the monoptic and dichoptic processing streams respond to the attenuation of signal strength in a similar manner.

The aim of the current study was to explore the determinants of the DI with a view to elucidating the underlying perceptual mechanisms. Operating characteristics of the DI under variations of inducer stimulus strength were measured across binocular, monoptic, and dichoptic presentation conditions to establish the role of monocular and binocular stages of visual processing. A center-surround configuration was used throughout so as to avoid binocular rivalry between inducer and test under dichoptic presentation. To give a broader indication of the effects of inducer strength on the DI, and because there is some evidence that the DI is greater at slow speeds (Braddick et al., 2002; Rauber & Treue, 1999), operating characteristics were measured at both a fast (4°/s) and a slow (0.5°/s) dot speed determined from initial pilot testing. Systematic interactions between dot speed and the stages of visual processing (binocular, monocular, and dichoptic) emerged at the individual observer level. Monoptically, the DI was, where present, always repulsive. Significant interocular transfer of the DI was also apparent in many participants in the dichoptic condition. In some cases it was typically repulsive and of a magnitude less than in monoptic viewing, as was anticipated. In other cases however, the DI that emerged was in fact attractive and often quite strong. Across all viewing conditions the DI was generally much greater for slower compared to faster speeds, similar to previous research (Braddick et al., 2002; Rauber & Treue, 1999).

The results reveal that a systematic exploration of the determinants of illusions such as the DI at the individual-observer level can reveal important functional properties of low-level visual processing that might otherwise go undetected (Nefs, O’Hare, & Harris, 2010).

General methods

Many aspects of the study were common to all experiments and are described in the following section. Deviations from these parameters are outlined in the respective sections of subsequent experiments.

Participants

There was a total of 18 participants in the current series of experiments (age range 21–33; seven female), including two of the authors (TC and RM), and 16 who were naïve to the theoretical motivation of the study. All participants were screened prior to participation using an Optec 2500 Vision Tester (Stereo Optical Co., Chicago) and were found to have normal (or corrected-to-normal) visual acuity, normal stereopsis (disparity thresholds ≤ 100 arcsec) and good binocular fusion. Informed consent was obtained from all participants according to procedures approved by the University of Sydney Human Research Ethics Committee.

Apparatus

Stimuli were generated using a Windows XP personal computer with an Intel i7 2600 CPU and AMD Radeon HD 6350 graphics card running MATLAB (The Mathworks, Natick, MA) and the Psychophysics Toolbox (Brainard, 1997; Pelli, 1997), driving a gamma-corrected 18-in. Viewsonic Graphics Series G90f cathode ray tube monitor with 1024 × 768 resolution and a refresh rate of 85 Hz. A chin rest was used to situate participants at a viewing distance of 57 cm from the monitor. Responses to stimuli were made using a standard computer keyboard. A circular black cardboard aperture (diameter 12 cm) was placed over the monitor frame to occlude any external visual cues to vertical.

Stimuli

The stimulus used to induce the DI had a center-surround arrangement (see Figure 1). The background of the display had a mean luminance of 48.6 cd/m². The target and inducer both consisted of linearly- translating RDKs centered upon a small black fixation spot (0.14° diameter), with the target presented in a circular aperture with a diameter of 3° and the inducer in a surrounding annulus with an outer diameter of 9°. Both target and surround had a uniform density of 6 dots/°². Dot stimuli had a Laplacian of Gaussian (LoG) luminance profile (sigma = 0.069°) and were randomly assigned to be either a full contrast increment or
coherence was fixed at 100%, and while coherence was varied, contrast was fixed at 100%. For both the contrast and coherence operating characteristics, the 100% contrast and 100% coherence blocks were therefore the same. The final estimate of the degree of target offset required for participants to report the target stimulus as moving upwards left or upwards right with equal likelihood in the interleaved leftwards and rightwards staircases defined the DI magnitude for a given stimulus strength, c, according to the following:

$$\text{DI}(c) = \frac{1}{2} (\mu_R - \mu_L)$$

where $\mu_R$ and $\mu_L$ represent the threshold of the psychometric function for the PSV at the end of the staircase for the rightwards and leftwards moving inducers, respectively. As the magnitude of the illusion was derived from the PSV, the procedure is resistant to baseline errors stemming from stimuli oblique to the cardinal directions (Rauber & Treue, 1999). The PSI procedure also returned a standard error of the DI, $\sigma_{DI}$, associated with each estimate of the PSV obtained at each step in the staircase, given by

$$\sigma_{DI} = \frac{1}{2} \sqrt{\sigma_L^2 + \sigma_R^2}$$

where $\sigma_L$ and $\sigma_R$ is the standard deviation of the posterior distribution of the 50% point of the psychometric function for the final step in the leftwards and rightwards staircases, respectively.

During each trial, the fixation point appeared on the screen for 750 ms prior to the onset of the RDK motion stimulus, which was presented for 500 ms together with the fixation point. After the motion stimulus was presented, the screen returned to a blank mean background luminance display and participants made a left or right forced-choice response using a computer keyboard to indicate the perceived direction of movement of the central target RDK (i.e., whether it appeared to move upwards and slightly to the right or slightly to the left), with no time limit imposed on responses.

Nonlinear least-squares regression was used to fit operating characteristic curves of the final DI values across contrast and coherence with a Naka-Rushton function of the form (see Pearson & Clifford, 2005):

$$\text{DI}(c) = I_{max} \left( \frac{c^n}{c^n + c_{50}^n} \right)$$

where DI(c) denotes the fitted DI as a function of inducer signal strength, c (contrast or coherence). $I_{max}$ is the highest value of the DI, and $c_{50}$ refers to the contrast or coherence value at which the illusion is at half its maximum magnitude. The exponent n determines the slope of the function. Because operating characteristics tended to show a more naturally
saturating function with increasing contrast, the $I_{\text{max}}$ parameters obtained for contrast were used to constrain function fits for coherence (as with Pearson & Clifford, 2005).

The use here of a fixed-direction inducer results in covariation of the test direction and the relative inducer-test direction difference. Fixing the relative inducer-test direction difference would have resulted in covariation of the test direction and the (absolute, with respect to vertical) inducer direction. Covariation of the test direction with the inducer (be it the relative inducer-test direction difference or the absolute inducer direction) is thus impossible to avoid when measuring the magnitude of the direction illusion.

The decision to use a fixed direction of the inducer, rather than fixing the inducer-test direction difference, was made for two reasons. First, when the absolute direction of the inducer is fixed it is always stimulating the same population of direction-selective neural mechanisms. When the relative direction of test and inducer is fixed, however, the population of neural mechanisms stimulated by the inducer varies with the direction of the test. Second, studies of adaptation typically use a fixed adaptor as its effect is cumulative over time and cannot be tied trial-by-trial to the test. Thus, our method facilitates comparability between the effects of simultaneous and successive contextual modulation (as in Wiese & Wenderoth, 2007).

A limitation of the use of a fixed direction inducer is that the inducer-test direction difference at the PSV will tend to covary with inducer signal strength. For example, if the magnitude of the DI at full contrast and coherence with a fixed inducer direction of 60° is, say, 10°, then the inducer-test direction difference at the PSV will be 50°. At the opposite end of the operating characteristic (i.e., approaching zero contrast or coherence) the magnitude of the DI will tend towards zero and the inducer-test direction difference at the PSV will be 60°. However, in terms of measuring operating characteristics of motion repulsion as a function of stimulus contrast or coherence what is arguably most important is that the method is explicit, replicable, and amenable to computational modeling. Both methods, fixed direction inducer and fixed inducer-test direction, satisfy these criteria.

**Pilot experiments**

A series of pilot tests were initially performed to determine the combination of parameters that produced the largest DI, in particular the inducer direction and dot speed. Marshak and Sekuler (1979) reported that matching the speeds of the two sets of dots produced the largest effect, while other researchers have found that the illusion was greatest when inducer dots moved faster than the target (Curran & Benton, 2003; Dakin & Mareschal, 2000), or slower (Braddick et al., 2002; Rauber & Treue, 1999). Even when target and inducer speeds are matched, slower stimuli appear to produce a greater effect (Braddick et al., 2002; Rauber & Treue, 1999). However, these studies involved a transparent motion paradigm where speed may have affected the differentiation of overlapping stimulus components (Masson, Mestre, & Stone, 1999), and it is not clear whether these findings also apply to the DI as measured with the center-surround configuration. Preliminary testing conducted here indicated that varying target and inducer speed independently provided no noticeable change, so target and inducer speeds were matched while mapping out tuning functions for speed and inducer direction in the illusion.

As with dot speed, the direction of movement of the inducer can also have an influence on DI magnitude. The DI elicited by transparent RDKs has been found to peak at around 20° with an inducing stimulus of 20°–30° (Marshak & Sekuler, 1979; Grunewald, 2004; Wiese & Wenderoth, 2007). Kim and Wilson (1997) identified 45° as the most efficacious inducer direction when using center-surround gratings, but it is unknown whether that would be applicable to the RDK stimulus. Finally, in addition to assessing dot speed and inducer direction, testing was conducted in order to ascertain whether illusory motion resulting from eye movements (Pomerantz, 1970) was affecting the DI measurements made with the current setup.

**Participants**

Piloting was conducted by two of the authors (TC and RM), both of whom were experienced psycho-physical observers.

**Stimuli and procedure**

Stimuli were viewed binocularly with surround contrast and coherence fixed at 100%. In order to collect speed and direction tuning data, dot speeds were varied at 0.5°/s, 1°/s, 2°/s, 4°/s, or 8°/s and with a surrounding inducer direction of 15°, 30°, 45°, 60°, 75°, 90°, 120°, or 180°. The 180° inducer direction was included as a control measure: Here the inducer dots moved directly downwards so there should not be any direction repulsion.

The effects of controlling for eye movements were investigated by presenting fast (4°/s) and slow (0.5°/s) moving stimuli with a 60° inducer direction in several new conditions. Participants viewed the stimulus through a monocular pinhole with either eye, monoc-
ularly with either eye, or binocularly at a reduced presentation interval of 153 ms, an insufficient time for a saccade to be generated in response to the stimulus (Robinson, 1965). The pinhole (diameter 6 mm and positioned 33 cm from the monitor, and hence 24 cm from the participant) was designed in such a way that an eye movement would result in the stimulus vanishing from view. During the monocular conditions, the untested eye was occluded with a dark eye patch.

Results and discussion: Pilot testing

The speed and direction tuning curves derived from the experiment can be seen in Figure 2. In both participants, the magnitude of the DI increased as dot speed was decreased, peaking at around 25° of repulsion for the lowest tested speed of 0.5°/s, at the most effective inducer directions. Examining the DI as a function of inducer direction showed that the effect peaked at an inducer direction of around 60°–75° across the majority of dot speeds, corresponding to an angular difference between inducer and test directions of 35°–50°. As expected, no DI was found with an inducer direction of 180°.

The results of the eye movement control conditions are plotted in Figure 3. A repulsion effect of a magnitude similar to that seen in the first pilot experiment (i.e., around 20°–25° at the 0.5°/s speed) occurred under all conditions tested. Given that in all cases the illusion magnitude was not noticeably reduced, it appears that eye movements were not influencing the direction repulsion experienced in either the 0.5°/s or 4°/s speeds.

The pilot tests showed that the largest magnitude of direction repulsion was obtained with an inducer direction of 60°–75°, so it was decided to adopt an inducer direction of 60°. Although past studies typically utilized faster dot speeds, the current study obtained the largest repulsion value at the slowest speed tested, 0.5°/s, with the effect consistently decreasing as the speed was increased. Further testing suggested that this result was not the product of tracking eye movements.

Figure 2. DI as a function of inducer direction and dot speed for the two observers. Negative values on the y axes correspond to direction attraction. Error bars indicate ±1 standard error of the illusion, σDI.

Figure 3. DI under monocular (left or right eye), monocular pinhole (left or right eye) and binocular 153 ms duration presentation conditions for the two observers. Error bars indicate ±1 standard error of the illusion, σDI.
in response to the slower motion stimulus, consistent with previous work showing that eye movements do not contribute to the illusion (Marshak & Sekuler, 1979).

**Experiment 1: Mapping the operating characteristics of the binocular direction illusion**

In this experiment, the operating characteristics of the DI were measured binocularly at the 0.5°/s dot speed, which appeared to produce a large direction repulsion effect, as well as the 4°/s dot speed, which yielded moderate DI magnitudes in pilot testing and has been commonly used in earlier research (Grunewald, 2004; Wiese & Wenderoth, 2010).

**Participants**

Nine subjects participated in this experiment, including two authors (TC and RM) and seven naïve participants (three females).

**Stimuli and procedure**

The details of the center-surround stimulus are described in the general method. The inducer direction was fixed at 60° and dots in both the center and surround drifted (in separate blocks) at 0.5°/s or 4°/s. Surround contrast or coherence was varied (in separate blocks) between 10% and 100%, in 10% increments. The apparatus and all other aspects of the stimulus were identical to that described in the General methods. Each participant completed 20 blocks (in random order) of the 60-trial staircases in total: 10 each for the contrast and coherence manipulations of stimulus strength.

**Results and discussion: Experiment 1**

Mean operating characteristics (Equation 3) were fitted to the mean data across the nine participants and are depicted in Figure 4. While a few participants exhibited no DI at the fast speed, the remainder showed a repulsive effect and all exhibited repulsion at the slow speed. Consistent with the pilot data, the 0.5°/s dot speed produced larger magnitudes of direction repulsion than the 4°/s speed.

Although there appeared to be some individual differences in the magnitude of the illusion, most participants exhibited some level of direction repulsion, on average producing saturating nonlinear operating characteristics with surround contrast or coherence. Investigation of the mean data (see Figure 4) showed that a negligible DI was occurring at levels of coherence.
below 40%. As a result, it was decided that further testing would use 40% as the lowest coherence level in order to ensure that data collected was diagnostic. The illusion appeared to saturate at fairly low contrast levels so all 10 contrast increments were retained for the measurement of operating characteristics in the dichoptic experiment, providing a larger margin for the dichoptic attenuation of the effect.

Experiment 2: Measuring the dichoptic direction illusion

Experiment 2a: Interocular transfer of the direction illusion

Earlier studies suggest that the DI is, on average, weakened with dichoptic presentation (Grunewald, 2004; Wiese & Wenderoth, 2007, 2010), though it remains a possibility that individual differences across participants might be obscuring or reducing the effect. The aim of Experiment 2 therefore was a close examination of any possible individual differences in interocular transfer of the DI in a dichoptic presentation setting.

Participants: Eighteen participants (seven female) were tested in this component of the study, the two experimenters (RM and TC) and 16 naive observers. This included all nine participants from Experiment 1.

Apparatus and stimuli: A mirror stereoscope was positioned in front of the monitor used in Experiment 1 in order to allow for monoptic and dichoptic presentation conditions in a similar set-up to that of Forte and Clifford (2005). The mirrors were first-surfaced with a flat reflectance spectra. A chin rest was used to position participants at a viewing distance of 57 cm from the monitor, including the optical pathway of the mirrors. Two 10-cm diameter, 50-cm long cardboard tubes with a nonreflective inner surface were positioned between the monitor and mirrors to ensure that no vertical reference cues were visible (Forte & Clifford, 2005).

A schematic representation of the stimulus as presented through the stereoscope is given in Figure 5. Stimuli were presented through the stereoscope in four conditions: left eye monoptic, right eye monoptic, left eye dichoptic, and right eye dichoptic. In the monoptic conditions, the combined center-surround stimulus was presented to the left (left eye monoptic) or right (right eye monoptic) eye and a blank background to the other eye. In the dichoptic presentation conditions, the target was presented to the left (left eye dichoptic) or right (right eye dichoptic) eye, and the surround inducer to the other eye. In all presentation conditions, the stimulus areas in each eye were framed by circular fixation locks in order to assist with binocular fusion. Fixation locks were 0.35° wide and consisted of black and white 9° sectors; black sectors were positioned on the left and right and white sections on the top and bottom of the stimulus to avoid presenting a precise cue to vertical (see Figure 5). The center-surround motion stimulus has been reported not to produce binocular rivalry (Wiese & Wenderoth, 2010) and in all conditions the center and surround were perceived together in a coherent whole, making it difficult for observers to distinguish between the interleaved presentation conditions. As in Experiment 1, the inducing angle was 60° and dots moved at 0.5°/s or 4°/s.

Procedure: Each block of the experiment consisted of eight interleaved staircases: leftwards and rightwards direction staircases (30 trials each) for each of the left eye monoptic, right eye monoptic, left eye dichoptic, and right eye dichoptic conditions (240 trials in total). In order to gauge the interocular transfer of the illusion, each participant completed a single block at the 0.5°/s and 4°/s speeds. Stimulus contrast and coherence were fixed to 100%.

Results: All participants reported that they did not experience binocular rivalry. Furthermore, naive participants were not aware that the task utilized four distinct presentation conditions, suggesting that the physically different center-surround arrangements were not utrocularly distinguishable.

Summaries of the distribution of the DI magnitude across conditions and eyes are depicted in Figure 6. Consistent with the binocular experiment, the mean DI magnitude across participants for both fast and slow speeds in the monoptic condition was positive (i.e., repulsive), with a substantially larger effect at the slow speed. However, in the dichoptic presentation conditions the mean effect was closer to zero or even negative, and the range of values appeared to include substantial magnitudes of negative repulsion, or direction attraction. There was also a wider spread of the DI at the 0.5°/s speed compared to the 4°/s speed.

The relationship between the magnitude of the illusion in left and right eyes is depicted in Figure 7; linear regression analyses were performed and regression lines were fit to the data wherever correlation coefficients were significant. DI in the left eye monoptic and right eye monoptic presentation conditions was significantly correlated, at both the 0.5°/s and 4°/s dot speeds. Similarly, illusion magnitude in the left eye dichoptic and right eye dichoptic conditions was significantly correlated at both the fast and slow speeds. It appears that there were no ocular imbalances or aberrations confounding the results; the consistency of the illusion magnitude across eyes suggests that the effects are reliable and not due to noise.

Paired sample t tests (two tailed) were used to compare the DI (averaged across eyes) between monoptic and dichoptic presentation conditions. At the
At a 4°/s speed, there was a significant difference between the monoptic (mean = 4.95°, SD = 3.64°) and dichoptic (mean = 1.51°, SD = 5.35°) DI, t(17) = 3.82, p = 0.001. A significant difference between the monoptic (mean = 21.01°, SD = 7.78°) and dichoptic (mean = −3.27°, SD = 12.92°) effect was also found at the 0.5°/s speed, t(17) = 8.03, p < 0.001. It appears that at both speeds, dichoptic presentation (on average) attenuated the magnitude of direction repulsion compared to its strength with monoptic presentation.

While the illusion at both the fast and slow speeds was significantly attenuated by dichoptic presentation, they nonetheless appeared to exhibit different patterns of interocular transfer, which can be characterized by plotting the dichoptic against the monoptic illusion for each eye (Figure 8). Linear regression analyses were performed to explore the relationship for each eye and regression lines are plotted where significant in Figure 8. At the 0.5°/s speed, monoptic and dichoptic illusion magnitudes were not significantly correlated in either the left or right eyes. However, at the 4°/s speed, monoptic and dichoptic illusion magnitudes were significantly correlated in both eyes.

The difference in interocular transfer between the fast and slow speeds is reflected in the sign of the illusion. While interocular transfer for the 4°/s dot speed was at zero or generally positive in almost all of the tested participants, approximately half exhibited negative dichoptic DIs in the 0.5°/s speed: a direction attraction effect. A small number of participants exhibited dichoptic attraction at the 4°/s speed, but this was relatively infrequent.
Figure 6. Box-and-whisker plots illustrating the range of the DI across presentation condition for the two eyes separately at the 0.5°/s and 4°/s speeds. The ends of each box mark the 25th and 75th percentiles and the bold central bar denotes the median illusion. Whiskers show the most extreme nonoutlier data points, whereas asterisks indicate individual outliers.

Figure 7. Scatter plots depicting left eye DI magnitude as a function of right eye DI magnitude at the 0.5°/s and 4°/s dot speeds in monoptic and dichoptic presentation conditions. Positive values on the x and y axes correspond to direction repulsion, whereas negative values indicate direction attraction. Each participant is represented by a single unique symbol; vertical and horizontal error bars for each data point indicate ±1 standard error of the illusion, $r_{DI}$, for the left eye and right eye, respectively. Correlations between left and right eye magnitude were significant in every condition ($p < 0.001$); solid blue lines indicate the fitted linear regression functions.
Experiment 2b: Operating characteristics for the monoptic and dichoptic direction illusion

The first component of Experiment 2 revealed substantial individual variability in the interocular transfer of the DI. Although the monoptic DI was consistently positive, participants appeared to be equally likely to exhibit repulsion or attraction when the stimulus was presented dichoptically at the 0.5°/s speed. Interindividual differences appeared to be smaller at the 4°/s speed, with most participants exhibiting repulsion or no illusion in the dichoptic condition, although a few nonetheless exhibited a dichoptic attraction effect. To attempt to clarify these findings, monoptic and dichoptic operating characteristics of the DI were measured at the 0.5°/s and 4°/s speeds.

Participants: The experiment included seven observers: two authors (RM and TC) and five naïve participants (three female). Four participants were tested at each speed; one participant (RM) was tested at both speeds. Participants were selected with the aim of attaining a reasonably representative picture of the individual differences observed in Experiment 2a: While some showed repulsive effects in the dichoptic presentation conditions at the speed where their operating characteristic was measured, others exhibited direction attraction.

Stimuli and procedure: Stimuli were identical to those used in Experiment 2a except contrast and coherence were varied between each block of the experiment. Participants completed 17 blocks of the task outlined in Experiment 2a: Seven for the coherence operating characteristic, with surround coherence ranging from 40%–100% in 10% increments, and 10 for the contrast operating characteristic, with surround contrast ranging from 10%–100% in 10% increments. The order of presentation of these blocks was randomized and interleaved across signal strength and presentation condition. To help better describe the form of the operating characteristics the monoptic and dichoptic data for each participant (averaged across the eyes) was modeled in the same way as with the binocular data (Equation 3). Results and discussion: Experiment 2b: The operating characteristics for contrast and coherence of the four observers at 0.5°/s are plotted in Figure 9. Similar to

![Figure 8](https://jov.arvojournals.org/pdfaccess.ashx?url=/data/journals/jov/933549/)
Experiment 2a, both repulsive and attractive effects were observed, manifesting in the operating characteristics as nonlinearly increasing or decreasing functions. For subject RM the contrast operating characteristic appeared to suggest a more pronounced illusion than with increasing coherence, while for TC and YO the increasing direction attraction was more evident with contrast manipulation. While one subject did not appear to exhibit any dichoptic effect (JF), others exhibited notable repulsion (RM) or attraction (TC, YO) in the dichoptic conditions.

Operating characteristics for contrast and coherence at $4^\circ/s$ are depicted in Figure 10. In subjects DKL, EM, and RM, interocular transfer did not appear to be
equivalent to a reduction in effective inducing contrast; although the binocular and monoptic effect saturated at intermediate levels of contrast, the dichoptic effect did not reach the same magnitude. In subject GK, little or no repulsion was found in the monoptic condition but substantial direction attraction was observed with dichoptic presentation, with the operating characteristic monotonically decreasing as inducer contrast and coherence were increased.

The introduction of dichoptic presentation conditions revealed substantial interindividual differences in the magnitude and sign of the DI. In the monoptic presentation conditions (as well as in the binocular condition from Experiment 1), individual differences were limited to the magnitude of the illusion, with all observers exhibiting either varying levels of direction repulsion or no effect. Interestingly, dichoptically presented stimuli were capable of producing direction...
attraction as well as repulsion. The dichoptic attraction effect appeared to be more common at the 0.5°/s speed, being shown by approximately half of the participants in Experiment 2a. At the 4°/s speed, fewer individuals exhibited an attractive effect. These effects were confirmed by the nonlinearly increasing or decreasing operating characteristics found in dichoptic repulsion and attraction respectively.

**General discussion**

The current study sought to characterize the DI across different speeds under binocular, monoptic, and dichoptic viewing conditions in order to explore the degree of signal strength reduction associated with dichoptic presentation through the examination of operating characteristics. The DI exhibited more extreme effects at the slowest speed tested, 0.5°/s, both in terms of its magnitude when measured binocularly and also the variability across subjects under dichoptic presentation. Many participants exhibited attractive rather than repulsive effects under dichoptic presentation, particularly at the 0.5°/s speed. While in general DI magnitude is larger at slower speeds (e.g., Braddick et al., 2002; Rauber & Treue, 1999), it is possible that the wider variability of PSVs measured in the 0.5°/s speed condition reflects a poorer direction sensitivity in general for slow compared to fast speeds. There is evidence that slower speed channels are higher in internal noise and have a lower sampling efficiency (Bogfjellmo, Bex, & Falkenberg, 2013). This may be related to the shorter total distance traveled for a slower moving field of dots. Either way, the greater variability and larger average magnitude in the 0.5°/s speed condition may be an indication that motion processing at slower speeds is more prone to the type of perceptual biases that can be revealed through behavioral measures such as those employed here.

The most effective inducing angle for producing a large DI differed somewhat from earlier research. While pilot testing in the current study found that angles of 60°–75° elicited the strongest direction repulsion of around 25°, corresponding to an angular difference between inducer and test directions of 35°–50°, Marshak and Sekuler's (1979) original study obtained the largest magnitude of the illusion using a 22.5° inducing angle in a transparent motion stimulus arrangement. Braddick et al. (2002), using a similar stimulus, found that the largest illusion magnitude was produced by a 45° inducer, while angles of 11.25° and 22.5° resulted in a small direction attraction effect. However, overlaid dot patterns presented with a small directional separation are perceived as a single surface moving in the vector average of the two directions, rather than as overlaid patterns moving in different directions (e.g., Felisberti & Zanker, 2005; Greenwood & Edwards, 2007; Mather & Moulden, 1980; Smith, Curran, & Braddick, 1999; Takemura, Tajima, & Murakami, 2011). Hence attraction measured at such small inducing angles may more accurately reflect a strategy of motion vector averaging, rather than direction attraction per se. This however should not be an issue for the center-surround configuration used here, due to the spatial separation of inducer and test stimuli.

Research on the speed tuning of the DI has largely focused on the effects of varying inducer speed while target speed was kept constant, with similarly inconsistent findings. While some researchers have found that using an inducer speed exceeding that of the target produced a greater effect (Benton & Curran, 2003; Dakin & Mareschal, 2000; Lindsey, 2001), others found no increase in magnitude with faster inducers (Marshak & Sekuler, 1979). The unique characteristics possessed by the transparent motion paradigm may have contributed to these inconsistencies. Research on the DI using overlaid RDKs must overcome the fundamental limitation that patterns moving across the same spatial region, if not sufficiently differentiated, are perceived as a single pattern rather than as independent transparent surfaces (Rauber & Treue, 1999; Yo & Wilson, 1992). Although the most commonly studied parameter for eliciting the perception of transparency is angular direction difference (Braddick et al., 2002; Marshak & Sekuler, 1979), a difference in speed can in itself result in segmentation; overlaid RDKs moving in the same direction but at different speeds are perceived as two distinct transparent surfaces (Masson et al., 1999). Given that inducer direction and dot speed are acutely important in ensuring that spatially coincident motions are perceived in such a manner that can elicit the DI, it is unsurprising that these parameters also affect the magnitude of the illusion. Beyond the threshold where the two surfaces are sufficiently differentiated to appear transparent, changes to speed or angular direction difference may nonetheless render more apparent their perceived separation, increasing the magnitude of the illusion. Correspondingly, differences between tuning functions measured in earlier studies utilizing this paradigm are likely to have been contributed to by differences in stimulus parameters, rather than differences in the mechanisms of the illusion per se.

The center-surround presentation method used in the current study does not require the extraction of motion from overlaid patterns as with the transparent RDK arrangements used in earlier work, which might explain some of the differences found here. This dissociation is reflected in the response characteristics of neurons in some motion-sensitive regions: Monkey
MT neurons respond differentially to transparent and non-transparent motion (McDonald, Clifford, Solomon, Chen, & Solomon, 2014; Snowden et al., 1991), and there is evidence that the response pattern of neurons in human area V3A are determined by the type of global motion presented (Koyama et al., 2005). On that basis, it is perhaps likely that the psychophysical dissociation between the two presentation methods reflects an underlying neurophysiological dissociation and the center-surround and transparent motion paradigms engage different neural mechanisms.

While the current study aimed to ascertain whether dichoptic presentation reduced the effective contrast of the stimulus or produced a more complex shift in the operating characteristic, the finding of dichoptic attraction cannot be easily explained by an attenuation of the signal or a change in gain (Pearson & Clifford, 2005). A small number of earlier studies on the DI have unearthed direction attraction effects but these findings tended to be of limited scale and magnitude, resulting in direction attraction being largely overlooked. Grunewald (2004) examined the dichoptic illusion using transparent RDKs with a range of inducing angles. Although he made no reference to attractive effects, a scatter plot depicting interocular transfer showed that all participants exhibited direction repulsion in the binocular condition but a small subset showed an attraction effect in the dichoptic condition (see figure 3 in Grunewald, 2004). Wiese and Wenderoth (2007) replicated this experiment and found dichoptic attraction at obtuse angles (greatest at $-5^\circ$ with a $150^\circ$ inducer) even after baseline effects were subtracted from measurements. The binocular illusion, in comparison, was entirely repulsive. Furthermore, after switching to a forced choice response paradigm to reduce measurement errors, an attraction effect of $-3^\circ$ was retained in dichoptic presentation when a $120^\circ$ inducing angle was used; a $30^\circ$ inducing angle produced no dichoptic DI. However, a subsequent experiment using a center-surround stimulus arrangement found no attraction effects (Wiese & Wenderoth, 2010). The current study found much larger effects in some participants; direction attraction reached $-11^\circ$ for subject GK at the $4^\circ$/s speed, and $-18^\circ$ for TC at $0.5^\circ$/s. Furthermore, these attraction effects were elicited by a $60^\circ$ inducer direction, whereas earlier researchers had found no attraction with similar parameters (Grunewald, 2004; Wiese & Wenderoth, 2007).

The method of stimulus presentation may have contributed to these differences. Apart from the current study, the center-surround RDK stimulus has only been presented dichoptically in one paper that the authors are aware of (Wiese & Wenderoth, 2010), with the remainder utilizing transparent motion (Chen et al., 2001; Grunewald, 2004; Marshak & Sekuler, 1979; Wiese & Wenderoth, 2007). Most strikingly, the interindividual variability in the sign and magnitude of the DI found in the current study illustrates the potential for aggregation of results to mask a highly variable but valid effect. In Experiment 2a, averaged across eyes, the dichoptic illusion at $0.5^\circ$/s had a mean of $-3.28^\circ$ ($SD = 12.92^\circ$), while the $4^\circ$/s condition had a mean of $1.51^\circ$ ($SD = 5.35^\circ$). Given how close these average values are to zero and the wide variability across participants, a cursory examination of the findings might suggest that no dichoptic effect occurred. For the slow speed, statistical analysis was consistent with this outcome; monoptic magnitude was not correlated with dichoptic magnitude. Even so, the large correlation between the left and right eye dichoptic conditions at both speeds suggests that there is consistency in individual participants' perceptual reports. Further examination revealed that both repulsive and attractive effects manifested as nonlinearly saturating operating characteristics (see Figures 9 and 10), a finding that would be negated entirely if data were averaged across participants. This may account for Grunewald’s (2004) conclusion that no DI occurred when stimuli were presented dichoptically. The current study broadly supports the findings of earlier researchers in establishing that attractive effects in the DI appear to be exclusively dichoptic (Wiese & Wenderoth, 2007). In addition, these results emphasize the importance of taking into account the sign of psychophysical interactions, in order to ensure that seemingly robust effects with broad interindividual variability are not hidden by aggregation (Nefs et al., 2010).

Under the differential processing model, the inferred background motion that contributes to the DI is calculated on the basis of the observed motions’ relative rather than absolute speeds (Dakin & Mareschal, 2000), a mechanism that does not account well for the speed and direction tuning characteristics obtained in the pilot experiments of the present study. In the binocular viewing condition, the magnitude of the illusion at a dot speed of $0.5^\circ$/s was approximately four times that elicited by the $4^\circ$/s speed, supporting earlier research associating slower speeds with a larger illusion magnitude (Braddick et al., 2002; Rauber & Treue, 1999). Although it could be argued that the $4^\circ$/s speed produced a smaller effect due to the reduction in effective contrast associated with faster motion stimuli (de Lange, 1958), earlier research on the DI suggests that effective contrast is reduced only at substantially faster speeds (Curran & Benton, 2003).

The complex pattern of interocular transfer found in the current study, with direction attraction emerging only in dichoptic conditions, is difficult to reconcile with theoretical accounts where the DI is attributed exclusively to local monocular or global binocular neural loci. Earlier research has found limited inter-
ocular transfer on the one hand (Wiese & Wenderoth, 2007, 2010) as well as evidence for global integration on the other (Benton & Curran, 2003). However, there remains the possibility that global, high-level processing is not limited to binocular areas, as suggested by traditional accounts (Maunsell & van Essen, 1983a, 1983b). Tailby, Majaj, and Movshon (2010) for instance found, using single-unit recordings in the macaque monkey, that some neurons in MT that exhibited pattern-sensitivity when presented with monoptic plaids lost this sensitivity when plaid components were presented dichoptically. Since similar dichoptic stimuli presented to human observers in the same study resulted in the perception of coherent pattern motion despite the occurrence of binocular rivalry, the ability of dichoptic presentation to negate pattern responding in single neurons suggests that pattern sensitivity in some MT cells may operate monocularly. Furthermore, research on motion-in-depth perception has provided evidence that 2-D plaid motion is extracted at a monocular locus prior to binocular recombination to form a 3-D percept (Rokers, Cormack, & Huk, 2009; Rokers, Czuba, Cormack, & Huk, 2011). This is supported by Guo, Benson, and Blakemore (2004), who found that a significant minority of V1 neurons responded to pattern rather than component motion. Although further research is needed to reconcile evidence for early spatial integration with the limited size of receptive fields in V1 (Hubel & Wiesel, 1974; Rokers et al., 2011), the growing research suggesting that global processing is not exclusively binocular may be useful in resolving inconsistencies in the DI literature. Similarly, the divergence of results at the dichoptic level in the current study suggests that the DI is produced by processing at multiple levels of the visual motion hierarchy. Future research would profit from an exploration of the binocularity of global integration and the neural locus of the DI by combining dichoptic presentation with manipulations that isolate global processing (see Benton & Curran, 2003).

Conclusions

The current study established that both speed and dichoptic presentation can substantially affect the quantitative properties of the DI. While binocularly and monocularly presented stimuli exclusively elicited a repulsive illusion (when present), dichoptic presentation resulted in attraction in approximately half the sample at the slow speed and a minority at the fast speed. These attraction effects were confirmed with the measurement of operating characteristics of the illusion. The large interindividual variability in the magnitude and sign of the illusion illustrates that caution should be used when aggregating data across multiple participants. The finding that speed and presentation condition have substantial effects on the DI suggests that it may be a useful tool in studying individual differences in the processing of motion and other visual attributes, particularly when comparing the interactions at monocular and binocular sites in the visual system.

Keywords: vision, motion, contextual modulation, direction repulsion, direction illusion, dichoptic stimuli, interocular transfer

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