

Towards a relative motion processing account of direction and speed perception

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Abstract

Spatial context influences the perceived velocity of moving objects. A number of theories have been proposed to account for a variety of visual motion phenomena that arise from such contextual effects. One theory proposes that the perceived direction and speed of a moving object are determined by an interaction of referenced (object-relative) and unreferenced (non-object-relative) motion components within the larger visual field. Presented here is an attempt to formalise a model based on this theory. The model dictates that the velocity of an object is perceptually decomposed into its constituent object-relative and non-object-relative component velocities. The two component velocities are differentially processed by the visual system such that the non-object-relative component velocity is underestimated with respect to the object-relative component velocity as a constant ratio. The research presented here investigates whether such differential processing does occur and whether it can explain various instances in which the velocity (direction and speed) of an object is misperceived. To test the model and to further explore the nature of the mechanisms involved, two well-known direction illusions are investigated: Duncker-type induced motion and the direction illusion arising in bidirectional transparent motion. In addition, a new illusion called the statically induced direction illusion is introduced. It is suggested that with some further development the proposed model will potentially account for a diverse range of visual motion illusions.

Statement of Candidate

I certify that the work in this thesis entitled ‘Towards a relative motion processing account of direction and speed perception’ has not previously been submitted for a degree, nor has it been submitted to any university or institution other than Macquarie University as part of the requirements for a degree.

I also certify that the thesis is an original piece of research and has been written by me. Any assistance that I have received in my research and in the preparation of this thesis has been appropriately acknowledged. Co-authors of the manuscripts presented herein are clearly shown on the respective manuscript title pages.

In addition, I certify that all sources of information are acknowledged in the thesis.

The research presented in this thesis was approved by the Macquarie University Ethics Review Committee; Reference number: HE27FEB2009-R06267.

Max Farrell-Whelan (student number 31241387)

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1 Introduction

1.1 Overview

This thesis examines aspects of human visual perception of motion. It is chiefly concerned with the spatial context-dependent nature of the perceived velocity (i.e. direction and speed) of objects moving within the fronto-parallel plane. Instances in which the perceived direction and/or speed of an object's motion is robustly affected by its spatial context have been well documented, but many questions remain regarding the determinants of these effects. Presented here is an attempt to account for these so-called illusions based on characteristics of relative motion perception. The current study proposes that such illusions result from the human visual system differentially processing referenced (object-relative) and unreferenced (non-object-relative) velocities. Empirical studies have shown that our visual system is more responsive to object-relative than to non-object-relative motion. Still others have shown that we perceive motion viewed object-relatively as having a higher velocity than the same veridical motion viewed non-object-relatively. The further suggestion that veridical velocities are decomposed into these two perceptually distinct components forms the basis of what is here termed the differential processing account. Whether this is a tenable account, and whether context-driven velocity perception can be attributed to differential processing is the overarching aim of the current thesis.

This dissertation centres on four empirical studies, each of which psychophysically investigates a different aspect of the proposed differential processing account. The first paper (Chapter 2) is a study of one instance of velocity misperception known as induced motion. It measures perceptual shifts in the direction of a moving target (test) resulting from the motion of a larger visual field (inducer) and seeks to determine whether the effect can be potentially

attributed to differential processing. The second paper (Chapter 3) investigates whether a second velocity misperception, the direction illusion (DI), is better explained by the current generally accepted account or by differential processing. The study introduces a novel illusion, called the statically induced direction illusion (SDI), to determine several characteristics of the proposed differential processing mechanism. The third paper (Chapter 4) attempts to formalise a model based on the differential processing account. The experiments test the model's quantitative predictions of shifts in perceived velocity (direction and speed) encountered in the SDI. The fourth, and final, paper (Chapter 5), in response to conflicting evidence in the recent literature regarding the neural locus of the DI, investigates the hierarchical order of processes associated respectively with the DI and the direction aftereffect (DAE). The DAE is a phenomenon often considered analogous to the DI, but arising from temporal rather than from spatial contextual determinants.

Before the proposed differential processing account can be fully understood and the significance of the research appreciated, some theoretical background involving an introduction to several key ideas is required. In the introductory section, a description is given of how the visual system is likely to facilitate context-dependent velocity perception through the integration and segmentation of motion signals. The introduction provides a theoretical framework for the journal articles that follow. While some scope for theoretical postulation and conjecture is allowed here, the articles themselves conform more rigorously to scientific guidelines, where speculative interpretations of results are avoided. Due to the format of this dissertation, with its inclusion of independent published and pre-published manuscripts, some repetition of ideas is inevitable. For the same reason, there is some inconsistency in the terminology and abbreviations used. For example, the statically induced direction illusion is abbreviated to SDI in some chapters but not in others, and induced motion is abbreviated to IM only in Chapter 2. The reader should

also understand that because the ideas presented here were developed over an extended period of time, manuscripts published prior to its full realisation (Chapters 2 and 5) make no explicit reference to the proposed differential processing account. The final section includes a summary of the findings and a discussion of their theoretical importance.

1.2 Visual motion perception

Our visual perception of motion largely defines our sensory experience of the world. The motion of an image on the retina provides information about a change that is taking place, either due to movement in the external environment or of the retina itself. Our perception of motion allows us to navigate as we move through the world. This it achieves by providing patterns of global 'optic flow' (Gibson, 1950) while simultaneously establishing object-ground segmentation wherever objects are perceived to move in relation to one another due to our own motion. Since the velocity of a stationary object on the retina during self-motion decreases with distance, the resulting motion parallax brings three-dimensionality to our universe (Nakayama & Loomis, 1974). Visual motion also allows us to interact with incredible precision and agility with other moving objects and organisms, including predators and potential meals. So vitally important is motion perception for survival, it seems, that all animals with vision have developed the capacity to process motion to at least some degree, which is not the case with colour vision, stereo vision and various other visual attributes (Dellen & Wessel, 2008; Koch, 2004; Nakayama, 1985). Many insects exemplify relatively simple organisms having devoted their limited visual processing resources to the perception of motion (e.g. Shoemaker, O'Carroll & Straw, 2001; Srinivasan, Poteser & Kral, 1999). It is perhaps partly because our survival as a species owes so much to this single attribute that the motion processing system has been investigated more thoroughly than any other sensory system (Albright & Stoner, 1995).

The early stage of motion perception is well understood as an extraction of localised, independent velocities in the form of changes in luminance on the retina. Beyond this lies a hierarchical neural network that is less well understood due to its physiological and functional complexity. Possibly its most important function is the combining of the localised inputs to form a coherent percept from which we may determine which motions to attribute to our own

movements through the world and which to attribute to the movement of objects around us. When motion percepts result from our own motion, generally we perceive large-scale, global motion of our surroundings. Conversely, the movement of other objects is perceived as a smaller-scale, local motion within a (usually stationary) more global frame of reference. This thesis is concerned with identifying characteristics of human motion processing involved in performing such tasks. To this end, it investigates how differences in the visual processing of motion due to movement of the observer (and/or the surrounding environment) and to the movement of external objects relative to the surrounding environment may account for instances in which the physical velocity of a moving object relative to the observer, termed veridical motion, is misperceived.

1.3 Visual motion illusions and differential processing

1.3.1 Induced motion

Visual misperceptions, or illusions, of velocity have been documented as early as Euclid (c.a. 300 B.C.E.), who described one of the most commonly experienced motion illusions thus: “If when certain objects are moved, one is obviously not moved, the object that is not moved will seem to move backward” (Wade, 1998, p.211). Euclid was describing what is now known as induced motion, and which in certain situations is also known as motion contrast (Reinhardt-Rutland, 1988). A commonly cited example of the phenomenon is the perceived movement of the moon induced in the opposite direction to drifting clouds (Porterfield, 1759). Harris & German (2008, p.695) describe understanding induced motion as being ‘important because it illustrates that motion perception involves much more than sensing motion from the retina of the eye. Its exploration gets at the heart of the problem of how the visual system assigns a reference frame against which other motion is measured. The key is to decide what is moving relative to what.’ Induced motion provides a striking and fairly robust example of the spatial context-dependent nature of velocity perception. It has been attributed to a discrepancy in our perception of two

kinds of motion (Gogel & Griffin, 1982; Harris & German, 2008; Kinchla, 1971; Rock, Auster, Schiffman & Wheeler, 1980; Wallach, 1965), which are referred to here as object-relative (OR) and non-object-relative (NOR) motion.

1.3.2 OR and NOR motion defined

The motion of an object whose frame of reference is another object (e.g. clouds, a point, line, textured background, etc.) is referred to as OR motion. When no other object is present and the observer therefore constitutes the only frame of reference, the motion is said to be NOR. NOR motion has also been referred to as ‘unreferenced’ (Johnson & Scobey, 1982), ‘uniform’ (Shioiri, Ito, Sakurai & Yaguchi, 2002), and ‘absolute’ motion (Snowden, 1992). OR motion has been known as ‘referenced’, ‘pattern-centric’ (Wade & Swanston, 1987) and simply ‘relative’ motion (e.g. Dellen, Clark & Wessel, 2005). Generally speaking, NOR motion arises from eye movements, or motion of the self, while OR motion indicates the movement of other objects. However, we can also rely to an extent on NOR cues to determine object motion, e.g. tracking a light in the dark, we are aware of its motion despite having no external visual reference frame, and on OR cues to perceive motion of the self, e.g. nearer objects move faster than distant objects during motion parallax. Our visual system thus relies on an interaction of OR and NOR motion information to create an intelligible perceptual representation of a dynamic scene.

1.3.3 Current objectives (in broad terms)

This thesis investigates whether such visual illusions as induced motion might be attributable to this perceptual interaction of OR and NOR motion. It is also aimed at determining whether other, separately reported instances of velocity misperception may be attributable to the same single underlying mechanism, which has been referred to by some as vector analysis (e.g. Gogel, 1979; Johansson, 1950; Wallach, Becklen & Nitzberg, 1985), and which is here termed differential processing. Differential processing refers to a computational process that has been

previously proposed to account for a number of context-determined velocity misperceptions. The hypotheses put forward here represent an extension of the earlier phenomenological theory within the context of a broader, more recent theoretical and empirical literature. It is proposed that the perceived direction and speed of a moving object is determined by the differential processing of NOR and OR motion. Differential processing entails that the veridical velocity of an object is perceptually decomposed into its constituent NOR and OR component velocities. The two component velocities are differentially processed by the visual system such that the former is underestimated with respect to the latter by a constant ratio. Due to this systematic imbalance, an object whose veridical velocity incorporates components of both NOR and OR motion will be perceived as having an altered velocity, i.e. direction and/or speed. This thesis investigates whether a hypothesis based on differential processing constitutes a credible proposition, and whether it can potentially explain a variety of spatial context-determined velocity misperceptions. An attempt is made to formalise a model based on this theory.

1.3.4 Properties of OR and NOR motion perception

In almost all real-world settings, any movement that we make, be it of our eyes, head, or entire body, results in changes in the light falling on our retinae. Retinal information is combined with signals from motor commands that control our eyes and head (efference copy or corollary discharge) (Guthrie, Porter & Sparks, 1983; Skavenski, 1990), and with proprioception and vestibular signals, all of which prevent us from attributing our own movement to that of the visual scene (Wertheim, 1994). Despite the compensatory effects of these extra-retinal signals, our perception of NOR motion is not entirely reliable (Raghunandan, Frasier, Poonja, Roorda & Stevenson, 2008; Turano & Heidenreich, 1999; Turano & Massof, 2001). If we view an object against a homogeneous background (Ganzfeld), such as a lone star in the night sky, it can appear to ‘wander’ around. This is the well-known autokinetic effect (Humboldt, 1850, cited in Conklin,

1957; Wade & Heller, 2003). This illusion is thought to arise from undetected motion of the self since it does not correlate highly with involuntary fixational eye movements (Wade & Heller, 2003). The autokinetic effect provides the simplest demonstration of the imprecision with which we perceive NOR motion.

Just as a stationary object can appear to move, an object in motion may appear stationary or as moving more slowly than it actually is (Blakemore & Snowden, 2000; Johnson & Scobey, 1982; Legge & Campbell, 1981; Leibowitz, 1955; Tyler & Torres, 1972). Again, this misperception may be due to our own undetected movements as we track the moving object through pursuit eye movements and/or motion-induced head position or postural change (Tanahashi, Ujike, Kozawa & Ukai, 2007). In addition to the apparent inaccuracy with which we perceive the NOR velocity of an object or visual scene (a stationary stimulus can be considered to have zero velocity), much of the literature suggests that, given a motion stimulus of ambiguous speed and direction, it will be perceived as the slowest motion consistent with the visual input, a tendency recently explained in terms of Bayesian statistical decision theory (e.g. Baker & Graf, 2008; Stocker & Simoncelli, 2005; Ullman, 1979; Wallach, 1935; Weiss, Simoncelli & Adelson, 2002). According to the proponents of several Bayesian models of motion perception, our visual system infers the most probable interpretation of a scene based on prior experience, and since most large-scale visual scenes are stationary, our visual system has developed a corresponding a priori expectation (prior) that the environment is stationary. One phenomenon arising from our prior of a stable environment isvection, the sensation of self-motion invoked by an expansive moving visual stimulus (e.g. Brandt, Dichgans & Koenig, 1973; Howard & Heckmann, 1989). A commonly experienced example ofvection is the sensation we have of our train pulling out of a station when it is in fact the adjacent train that is moving.

In contrast, we are much more sensitive in our perception of OR motion. Thresholds for the detection of OR motion have been found to be much lower than those of NOR motion (Lappin, Donnelly & Kojima, 2001; Legge & Campbell, 1981; Leibowitz, 1955; Mack, Fisher & Fendrich, 1975; Shioiri et al., 2002; Smeets & Brenner, 1994; Snowden, 1992; Sokolov & Pavlova, 2006), and direction discrimination thresholds are also lower for OR than for NOR motion (Beardsley & Vaina, 2008). A brief summary of these studies can be found in Chapter 4. Intuitively, it makes sense that we should be more sensitive to, and therefore more precise in our perception of, OR than NOR motion because while the processing of NOR velocities must combine extra-retinal signals with retinal signals, the processing of OR velocities operates on retinal signals alone. Raghunandan, Frasier, Poonja, Roorda, & Stevenson (2008) found only partial compensation for the effects of retinal jitter from fixation eye movements on discrimination thresholds of NOR motion, while OR motion thresholds were unaffected by such retinal jitter, possibly because all elements within a visual scene are equally affected by displacements of the retinal image, whether from retinal jitter or any other retinal movement, so the perceived position and motion of one object relative to another goes unchanged. According to Bayesian inference theory, because our experience tells us that objects (rather than expansive scenes) tend to move, we will not have developed a strong prior that objects are stationary. The prior should thus have little bearing on our perception of OR motion. Bayesian theory also dictates that the more ambiguous a perceived speed, the greater the influence of the prior. Because we are more sensitive to OR motion than to NOR, OR percepts are less ambiguous. OR percepts are consequently less susceptible to the influence of a prior expectation, resulting in a more accurate (closer to veridical) speed percept. Bayesian models therefore suggest that an object with a given veridical velocity when seen in the absence of contextual cues, i.e. in NOR motion, should be perceived as having a lower speed than when viewed in the presence of

contextual cues, i.e. in OR motion. Psychophysical evidence shows that this is indeed the case (e.g. Blakemore & Snowden, 2000; Brown, 1931; Gogel & McNulty, 1983; Nguyen-Tri & Faubert, 2007; Norman, Norman, Todd & Lindsey, 1996). A brief summary of these studies can be found in Chapter 3. Further evidence suggests that the comparative underestimation of NOR velocity is a constant proportion of perceived OR velocity (De Bruyn & Orban, 1999).

1.4 Motion integration and segmentation

The multiplicity of movement constantly going on around us presents our sensory system with a very complex computational task. The retinal image is initially fragmentary, with the visual input dispersed across literally millions of minute individual photoreceptors. An intelligible perceptual representation of a dynamic scene first requires the integration of these discrete positional signals over space and time, producing local motion signals that can then be integrated into a unified global motion construct (Movshon, Adelson, Gizzi & Newsome, 1985; Williams & Brannan, 1994). Motion integration is thus a hierarchical pooling process, whereby similar motion signals are grouped together into a single coherent motion while those that are sufficiently dissimilar are simultaneously segmented, allowing discrimination between motions of different velocities (Albright, 1984; Born & Bradley, 2005).

1.4.1 Component velocity dissociation

An early approach to understanding the perceptual principles governing integration and segmentation was introduced by the Gestalt movement (see Feldman, 2001; Wertheimer, 1923/1955), whose central dictum was summed up by Gunnar Johansson: “Elements... in motion on the picture plane of the eye are always related to each other” (Johansson, 1973, p.205). Developing Gestalt notions of how motion percepts are determined by the context of the entire visual scene, Johansson devised a set of principles to describe tendencies governing human perception of relative (and non-relative) motion. The most important of these principles, which

would inspire his well-known later work on biological motion perception (see Johansson, 1973), he referred to as the dissociation of systems of reference, which implies that, “equal simultaneous motion vectors can be mathematically abstracted [and] these components are perceptually isolated and perceived as one unitary motion” (Johansson, 1973, p.205). Johansson (1950) demonstrated this principle in a display with a homogeneous background against which two dots moving orthogonally to each other, one vertically and one horizontally, towards a point of intersection appear instead to be moving directly toward each other along the diagonal (Figure 1). Observers also detected an orthogonally oriented unitary motion of the two dots together, although this “secondary” (Johansson, 1950, p.7) motion was less conspicuous. There is thus a dissociation of the common and unique motion components. The common motion component becomes a moving reference system, and the motion unique to each element is perceived relative to that system. The distinction between common and unique motion parallels the earlier distinction between NOR and OR motion.

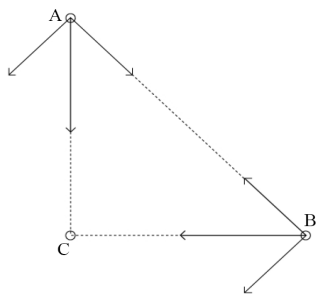


Figure 1. Schematic diagram showing the vector analysis principle of dissociation of systems: Two dots (A and B) moving orthogonally, one vertically and the other horizontally, towards a common point (C) are perceived instead as moving directly towards each other along the diagonal while at the same time moving as a unitary system along a second diagonal, orthogonal to the first (Johansson, 1950).

While Johansson’s dissociation of systems is a purely phenomenologically driven assessment of motion perception, as mentioned earlier (Section 1.3.4), there is evidence in the literature supporting the notion that NOR and OR motions are processed differently by the visual

system. These studies suggest the involvement of at least partially distinct neural systems in the extraction of NOR and OR motion. Further evidence that NOR and OR motion have separate neural substrates comes from developmental studies, which have found that infants show different developmental trajectories in their sensitivity to NOR and OR motion (e.g. Banton & Bertenthal, 1996). Despite the empirical support for Johansson's assertions, the integrity of his principle of the dissociation of systems rests on the further assumption that the visual system is somehow capable of separately extracting and processing NOR and OR component velocities from a single stimulus. Johansson's definition therefore refers not to NOR and OR veridical motions but to NOR and OR motion components that he presumes to have been perceptually dissociated and which together constitute a single veridical trajectory. Studies of induced motion may provide some indication that the visual system distinguishes between NOR and OR velocity components. Since induced motion was first demonstrated in a laboratory (Duncker, 1929/1955), various stimulus configurations have been used to induce changes in an object's perceived motion trajectory (Gogel, 1979; Wallach, Bacon & Schulman, 1978; Zivotofsky, 2004). These studies explicitly report that the perceived velocity of an object results from the vector sum of its veridical velocity and the velocity induced in the object opposite the inducer direction. Thus, at some stage our visual system seems capable of combining these components seamlessly to produce the single perceived trajectory (e.g. Gogel, 1979; Takemura & Murakami, 2010; Wallach et al., 1985). Wallach, Becklen and Nitzberg (1985) referred to this phenomenon as 'process combination'. However, no study thus far has satisfactorily addressed the important question of whether the dissociation and differential processing of NOR and OR components determines perceived velocity. Addressing this question is one of the central aims of the current studies.

1.4.2 Motion transparency and the direction illusion (DI)

One experimental stimulus often used in the study of motion integration processes is that of transparent motion. A commonly implemented transparent motion display is the bi-directional random-dot kinematogram (RDK) (Marshak & Sekuler, 1979; Mather & Moulden, 1980), which comprises two sets of spatially interspersed random dots scrolling continuously across the fronto-parallel plane (a screen) in two different directions (see Figure 1 in Chapter 5). RDKs allow the study of “pure” motion integration and segmentation (Lorenceau & Zago, 1999; Wallace & Mamassian, 2003) because observers must rely only on motion cues to perceptually segment the two sets (Snowden & Verstraten, 1999). Two teams of researchers studying characteristics of transparent motion in bidirectional RDKs reported that the angle between the two directions is perceptually exaggerated (Marshak & Sekuler, 1979; Mather & Moulden, 1980). This phenomenon is here referred to as the direction illusion (DI), although it has also been known as motion repulsion (e.g. Chen, Meng, Matthews & Qian, 2005). Both Marshak and Sekuler (1979) and Mather and Moulden (1980) attributed the DI to a shift in the response distribution of populations of cells sensitive to specific directions of motion. This is known as the distribution-shift model (Mather, 1980), which is discussed in some detail in Chapter 3. Simply put, populations of motion-sensitive cells are direction-tuned such that they respond maximally to a particular veridical direction and gradually less so to increasingly divergent directions. Each cell’s response distribution can be represented by an approximately Gaussian distribution with its peak corresponding to the cell’s preferred direction (Albright, 1984). When two similar directions of motion are presented simultaneously, as in a bidirectional RDK, and cells with different tunings are stimulated, they inhibit each other causing a mutual distortion in their response distributions. This results in a shift in each of the perceived directions, such that they appear “repelled” from each other. The distribution-shift model is based on physiological and

psychophysical evidence (see Snowden, Treue, Erickson & Andersen, 1991), and has become widely accepted as the mechanism underlying the DI (e.g. Braddick, Wishart & Curran, 2002; Chen, Matthews & Qian, 2001; Curran, Clifford & Benton, 2006; Curran, Clifford & Benton, 2009). The tenability of the distribution-shift model is tested in Chapter 3.

1.4.3 Do the DI and induced motion share a common mechanism?

In first reporting the DI, Marshak and Sekuler (1979) considered whether it might be a novel manifestation of induced motion, but they rejected this hypothesis on two counts. First, they argued that while induced motion can be invoked with large directional differences between the inducing and test stimuli, they found that the DI was eliminated when the directional difference between the two sets of dots exceeded 90° . Subsequent DI studies, however, have shown that the phenomenon does occur at directional differences far greater than 90° (Dakin & Mareschal, 2000; Grunewald, 2004; Wiese & Wenderoth, 2007). Second, Marshak and Sekuler found that the DI was speed-tuned, with the peak effect occurring when the two sets of dots were of equal speeds, a finding that is in approximate agreement with other DI studies (Curran & Benton, 2003; Dakin & Mareschal, 2000; Lindsey, 2001; Marshak & Sekuler, 1979), and they claimed that induced motion could not account for this observation. However, induced motion studies invariably utilise one of two distinct configurations, which tend to produce distinct results (e.g. Day & Dickinson, 1977). Marshak and Sekuler (1979) refer to the frame-and-spot display, in which the displacement of a surrounding frame induces movement in a small central point (e.g. Duncker, 1929/1955). However, bidirectional RDKs more closely resemble what is termed a fixed boundary display, in which an inducing pattern scrolls within a fixed region with no overall displacement (e.g. Tynan & Sekuler, 1975; Zivotofsky, 2004). Motion induced in such displays is often referred to as motion contrast (e.g. Reinhardt-Rutland, 1988; Zhang, Yeh & De Valois, 1993). Such studies have found induced motion to be speed-tuned, with a maximum

effect occurring when the test and inducer are of equal speed (Baker & Graf, 2010; Becklen & Wallach, 1985; Tynan & Sekuler, 1975; Wertheim & Paffen, 2009). Thus, the possibility that the DI shares a common underlying mechanism with induced motion cannot be ruled out on the basis of the above arguments. On the contrary, numerous parallels can be drawn between aspects of induced motion and the DI. For instance, induced motion and DI studies have both found that reducing the velocities in the display increases the magnitude of the respective illusions considerably (Braddick et al., 2002; Duncker, 1929/1955; Levi & Schor, 1984; Rauber & Treue, 1999; Rock et al., 1980; Wallach & Becklen, 1983). Moreover, both induced motion and the DI are contrast-dependent (Kim & Wilson, 1996; Kim & Wilson, 1997; Levinson, Coyne & Gross, 1980; Murakami & Shimojo, 1993; Raymond & Darcangelo, 1990) and both are robust to different fixation conditions and eye movements (e.g. Marshak & Sekuler, 1979; Rauber & Treue, 1999; Reinhardt-Rutland, 1988; Zivotofsky, 2004). However, the two phenomena are reportedly affected differently by disparity. Induced motion has been found to attenuate with increasing inducer-test depth separation (Gogel & Koslow, 1971; Heckmann & Howard, 1991; Marshak & Sekuler, 1979; Murakami, 1999; Zivotofsky, 2004). If induced motion and the DI have common mechanisms, the DI should also be reduced by sufficient depth separation of its component RDKs. Hiris and Blake (1996) reported no significant effect of disparity differences between the component RDKs (both crossed and uncrossed) on the size of the DI. However, their data reveal signs of a trend towards a gradual decrease in the DI with increasing depth separations. Since they used only a limited range of disparities (only up to 8 min arc), there is a distinct possibility that, had they used a larger range of depth separations comparable to those used in the induced motion studies (up to 20 min arc), they would have found a significant effect.

When Marshak and Sekuler proposed, and quickly rejected, that induced motion and the DI share a common mechanism, they may not have given sufficient consideration to what the precise characteristics of that mechanism might be. If induced motion can be attributed to an underestimation of the speed of the NOR component in the display (with respect to the OR component), as is generally thought, then to attribute the DI to the same mechanism potentially involves a Johansson-type component velocity dissociation. Previous studies have demonstrated that the type of phenomena described by Johansson exhibit identical qualities to those of induced motion (Gogel & Koslow, 1971; Gogel & MacCracken, 1979; Wallach, 1965; Wallach et al., 1985), and we have recently found that a dichoptically invoked Johansson-type illusion, in which the inducing and test stimuli were presented separately to each eye, yielded an effect 80% as large as when both stimuli were presented to the same eye. The 80% inter-ocular transfer (IOT) is comparable to IOT effects found in some IM studies (e.g. Day & Dickinson, 1977). The difference between most induced motion displays and Johansson-type displays is that the former consist of component velocities that lie along a common one-dimensional trajectory, while component trajectories in the latter are orthogonal. Dakin and Mareschal (2000), recognising this, adopted Johansson's model to account for the DI, proposing that the NOR and OR motions of the two sets of dots are extracted as separate orthogonal components (see Figure 2). Determining whether a single mechanism, namely the differential processing of NOR and OR component velocities, can potentially account for both induced motion and the DI is one of the central objectives of this dissertation.

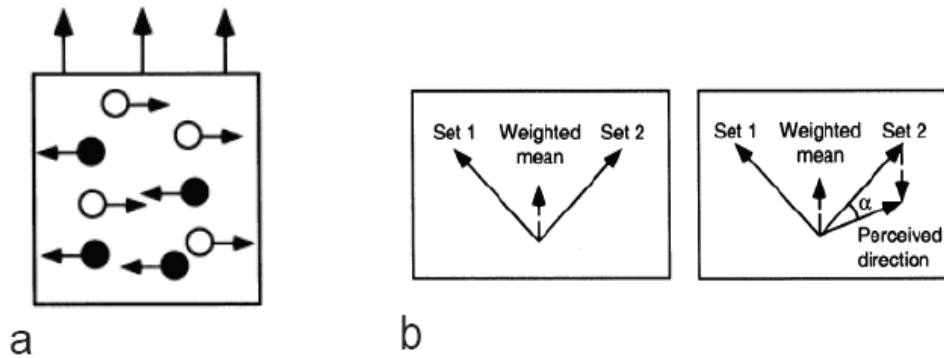


Figure 2. (a) The two directions in a bidirectional RDK as a dissociation of horizontal OR motion and vertical NOR motion. (b) Differential processing according to Dakin and Mareschal (2000) involves a two-stage process: the NOR component velocity is first inferred as the vector average (weighted mean) of all motion in the display. The underestimated NOR component speed is then vectorially subtracted from the veridical trajectories of the two dot sets, resulting in a direction shift (α) (from Dakin & Mareschal, 2000).

1.5 The visual motion processing pathway

The fate of any theory of visual perception is ultimately determined by the physical limitations of the visual apparatus. Some insight into the key processing stages involved in the integration and segmentation of motion signals is therefore required. Neurophysiological descriptions of the human visual system have largely been inferred from studies of the homologous macaque visual system (Maunsell & Newsome, 1987), to which the following cortical structures pertain.

The retinal photoreceptors responding to the temporal modulation of luminance feed into a network of bipolar, horizontal and amacrine cells, which converge on the ganglion cells (Vaney, He, Taylor & Levick, 2001). Signals are then transmitted to the lateral geniculate nucleus (LGN), where partial separation of the motion processing stream from that of other visual modalities, namely colour and form, takes place (Born & Bradley, 2005). Motion detection mechanisms are first encountered at the cortical level (Albright & Stoner, 1995). The simplest model of a motion detection mechanism is referred to as a Reichardt detector, which operates by

combining two retinal inputs with a delay introduced to one of the inputs such that a spatiotemporal comparison computation can be made (Nishida, 2011).

1.5.1 Hierarchical processing

Signal integration in the main motion-processing pathway can be thought of as approximating a three-stage process, where each successive stage pools signals from the preceding stage. Neurons in all three stages are directionally selective, i.e. they respond preferentially to a particular direction of motion (Albright & Stoner, 1995; Desimone & Ungerleider, 1986; Hawken, Parker & Lund, 1988; Movshon & Newsome, 1996; Tanaka, Hikosaka, Saito, Yukie, Fukada & Iwai, 1986). Early processing occurs in primary visual cortex (V1) (Livingstone & Hubel, 1987), and involves the extraction of spatially localised, small-scale velocity signals. About 30% of V1 cells are direction selective (De Valois, Yund & Hepler, 1982). These signals are integrated at a second stage into a more global, full-field representation in the medial temporal area (MT) (Anderson, Binzegger, Martin & Rockland, 1998; Huk & Heeger, 2002; Movshon & Newsome, 1996). Here, nearly all neurons (~95%) exhibit direction selectivity (Albright & Stoner, 1995) and, unlike a considerable proportion of cells in V1, are exclusively binocular, meaning that they combine signals from both eyes (e.g. Zeki, 1980). A further stage of pooling occurs in the medial superior temporal area (MST) (Ungerleider & Desimone, 1986). The neurons at each stage have increasingly larger receptive fields, which at the cortical level are known as classical receptive fields (CRFs) (e.g. Albright & Desimone, 1987; Huk, Dougherty & Heeger, 2002; Tootell, Mendola, Hadjikhani, Liu & Dale, 1998). The size of foveal V1 CRFs has been measured to subtend between ~0.2 and ~0.5 deg of visual angle at the fovea (Bair, Cavanaugh & Movshon, 2003; Dow, Snyder, Vautin & Bauer, 1981; Gur & Snodderly, 2007; Kagan, Gur & Snodderly, 2002; Orban, Kennedy & Bullier, 1986), and expand with increasing eccentricities (Bair et al., 2003). MT CRFs measure between ~2 and ~5 deg at the

fovea and are up to ~10 times the size of V1 CRFs at any given eccentricity (Albright & Desimone, 1987; Eifuku & Wurtz, 1998; Gattass & Gross, 1981; Mikami, Newsome & Wurtz, 1986; Tanaka, Sugita, Moriya & Saito, 1993). Foveal MST CRFs are larger again, ranging from ~4 to ~30 deg (Eifuku & Wurtz, 1998).

1.5.2 The aperture problem

Because they possess very small CRFs and therefore respond to motion within a spatially limited region of the visual field, V1 cells encode velocities that do not necessarily correspond to an object's veridical motion. This is known as the aperture problem (Adelson & Movshon, 1982; Wallach, 1935), illustrated in Figure 3. In the diagram, a plaid, which is a rigid two-dimensional stimulus formed by the superimposition of two orthogonal gratings, has a rightward veridical motion. When the contour of a single component grating crosses a CRF, only the motion orthogonal to that contour can be detected. In the diagram, the CRFs respond respectively to motion directions of 45° clockwise (CW) and counter-clockwise (CCW) of rightward horizontal. Information about the actual motion of the contour is thus under-constrained and therefore ambiguous. Only the integration of information from multiple CRFs can resolve the ambiguity by combining signals from various parts of the stimulus. Because a plaid is defined by contours in two dimensions, through integration the plaid is constrained to one possible direction of motion, eliminating the ambiguity inherent in the aperture problem. The substrate of veridical plaid perception is thought to be within MT, where the V1 afferents are integrated (Movshon et al., 1985; Rust, Mante, Simoncelli & Movshon, 2006; Smith, Majaj & Movshon, 2005).

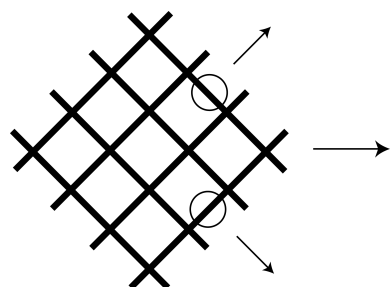


Figure 3. The aperture problem: V1 CRFs (circles) respond to the velocities of the two grating components, which have directions 45° CW and CCW of the plaid's rightward velocity. Resolving the aperture problem requires the integration of information from multiple V1 CRFs.

1.5.3 The CRF-surround mechanism

Visual motion stimulation from areas beyond the CRF, in what is known as the surround, can also modulate a neuron's activity. The surrounds in V1 are much larger than the CRF and are likely to derive from MT through feedback signals (Angelucci, Levitt, Walton, Hupe, Bullier & Lund, 2002; Cavanaugh, Bair & Movshon, 2002; Harrison, Stephan, Rees & Friston, 2007; Sullivan & de Sa, 2006), and Born and Bradley (2005) have suggested that MT surrounds signal feedback from higher tier areas, such as MST. Many neurons with the CRF-surround configuration respond maximally when motion in the surround has a different velocity (direction and/or speed) from motion in the centre and are inhibited when the velocities are the same. Such cells have been found in abundance within all three motion processing stages, V1 (Bair et al., 2003; Hammond & MacKay, 1981; Jones, Grieve, Wang & Sillito, 2001; Levitt & Lund, 1997; Tanaka et al., 1986; Zipser, Lamme & Schiller, 1996), MT (Allman, Miezin & McGuinness, 1985; Born & Tootell, 1992; Tanaka et al., 1986; Xiao, Raiguel, Marcar & Orban, 1997) and MST (Eifuku & Wurtz, 1998; Tanaka et al., 1993). Because they respond best to velocity discontinuities between their CRF and surround, such cells are responsible for velocity segmentation and are thus thought to be the mechanism underlying OR motion extraction and perception (e.g. see Murakami & Shimojo, 1996; Shioiri et al., 2002). Conversely, cells that respond best to a single velocity presented to both the CRF and surround are thought to facilitate the extraction and perception of large-scale NOR motion. Physiological studies have found that CRF-surround interactions are contrast-dependent, with surround modulation stronger at high contrast and spatial summation for global motion more pronounced at low contrast (e.g. Levitt & Lund, 1997; Tadin & Lappin, 2005).

1.5.4 The neural locus (loci) of differential processing

Results from several studies suggest that the limiting scale of OR motion perception corresponds well with the size of the foveal V1 CRF-surround (Lamme, Van Dijk & Spekreijse, 1993; Masson, Dodd & Enns, 2009; Matthews, Geesaman & Qian, 2000; Mestre, Masson & Stone, 2001; Murakami & Shimojo, 1996; Nawrot & Sekuler, 1990; Qian, Andersen & Adelson, 1994; Van Doorn & Koenderink, 1982). Qian et al. (1994) introduced a bidirectional RDK in which each dot moving in one direction was locally paired with a dot moving in the opposite direction. When the dot pairs were confined to a 0.4 deg region, thereby balancing the local signal, the percept of transparent motion became one of ‘motionless flicker’. A replication of the study produced the same effect but with smaller spatial restrictions of 0.25 deg (Wishart & Braddick, 1997). Matthews et al. (2000), using orthogonally moving dots, found that the percept of transparency (and the DI) occurred reliably only when the average distance between the orthogonally moving elements exceeded 0.3 deg. Matthews et al. (2000) further found that when the dots were precisely paired, unidirectional motion in the average direction was perceived, a finding corroborated by both Qian et al. (1994) and Curran and Braddick (2000). The results imply that the motionless flicker perceived in Qian et al.’s (1994) study was also due to an averaging of the opposite motions. Thus, at a sufficiently small scale that corresponds with the size of a V1 CRF the visual system seems incapable of segmenting velocity discontinuities (OR motion) and instead integrates them. Evidence indicates that cells in higher tiers such as MT and MST may process coherent, larger-scale motion by collating the local motion information from V1 (Braddick, 1993). MT neurons respond well to the coherent unidirectional motion of multiple elements (Allman, Miezin & McGuinness, 1990; Snowden et al., 1991), whereas V1 neurons do not (Allman et al., 1990), and the perception of global motion has been found to match activity in MT rather than V1 (Britten, Shadlen, Newsome & Movshon, 1992; Newsome,

Britten & Movshon, 1989; Stoner, Albright & Ramachandran, 1990). Although locally paired bidirectional stimuli produce a percept of the vector average velocity, a V1 direction-selective cell responds equally to motion in its preferred direction whether presented alone or locally paired with a second motion in the opposite direction (Qian & Andersen, 1994), while activity in MT cells tends to be suppressed by the addition of the second, anti-preferred motion (Qian & Andersen, 1994). Therefore, the vector average percept arising from locally paired velocities is likely to result from integration at the later stage of processing. MT cells are also suppressed, though to a lesser degree, by locally unpaired bidirectional dot patterns perceived in transparent motion, such that each cell's response is less than the sum of its responses to the component stimuli (Britten & Heuer, 1999; Ferrera & Lisberger, 1997; Recanzone, Wurtz & Schwarz, 1997; Snowden et al., 1991; Treue, Hol & Rauber, 2000). Potentially, then, the NOR component is extracted at this stage as an average of the motions in a display.

Symons, Pearson, and Timney (1996) found evidence for early OR motion processing and later NOR motion processing with the motion aftereffect (MAE). The MAE is the perceived motion in the opposite direction to a motion stimulus upon offset of that stimulus following adaptation (Wohlgemuth, 1911). They tested the duration of an MAE with a stationary test stimulus after adaptation to either NOR or OR motion. The NOR stimulus configuration consisted of a central motion stimulus presented alone, while in the OR condition it was surrounded by a static annulus. They tested both under dichoptic conditions, where the adapting and test stimuli are presented to different eyes, and found that after monocular adaptation to NOR motion an MAE was observed in the contralateral eye. Because MT cells combine signals from both eyes (e.g. Zeki, 1980), the finding suggests that the NOR motion had stimulated cells at this later processing stage. They also found that while OR adaptation, in comparison to NOR adaptation, enhanced the MAE in the ipsilateral eye, it failed to enhance the MAE in the

contralateral eye. This finding suggests that OR motion processing involves an early stage of processing before binocular integration, implicating activity in V1. In a binocular rivalry study, Paffen, te Pas, Kanai, van der Smagt, and Verstraten (2004) looked at the different effects between matched and opposite directions of centre-surround grating stimuli in both monocular and dichoptic conditions. Implementing all possible combinations, they found that centre-surround gratings moving in opposite directions were the most dominant percept. This finding further attests to the visual system's greater sensitivity to OR rather than NOR motion. Moreover, the dominance was significantly greater when both centre and surround stimuli were presented to the same eye. Since the effect was mostly monocular, V1 cells are once again implicated in the processing of OR motion.

1.5.5 The neural locus (loci) of the DI

Findings from several DI studies (see Chapter 5 for a comprehensive review) indicate that the illusion arises from early processing in V1 (Grunewald, 2004; Hiris & Blake, 1996; Marshak & Sekuler, 1979; Wiese & Wenderoth, 2007; 2010), while other studies attribute the effect to later processing in MT (Benton & Curran, 2003; Curran et al., 2009; Wilson & Kim, 1994). The discrepancies have led some researchers to postulate the involvement of more complex interactions between multiple stages of the processing pathway (Wiese & Wenderoth, 2010). It should be noted that these studies are concerned with locating the neural processes driving the DI rather than with identifying the characteristics of the mechanism involved and, as mentioned earlier, the DI is generally attributed to a shift in the response distributions of direction-selective cell populations, rather than to differential processing. If it is established that such velocity misperceptions as the DI and induced motion essentially share a common mechanism in differential processing, evidence relating to the neural mechanisms involved in NOR and OR motion processing may help to unravel the mystery surrounding the DI's neural substrate. While

most of the work presented here is aimed at investigating the possibility that they do both arise from differential processing, the final study (Chapter 5) approaches the question of the DI's neural locus directly and, in the tradition of the studies outlined above in the current section, investigates the hierarchical order of processing stages underlying the DI and a putatively related phenomenon, the direction aftereffect (DAE).

2 A study of induced motion

Induced motion is one of several visual motion phenomena that have been attributed in some way to the comparative underestimation of the NOR component velocity, (e.g. Duncker, 1929/1955; Gogel, 1979; Gogel & Tietz, 1976; Proffitt, Cutting & Stier, 1979; Wallach et al., 1985). In the past, induced motion has usually been measured only as it arises in stationary or orthogonally drifting stimuli. Exceptions are studies on rotational induced motion (Anstis & Reinhardt-Rutland, 1976; Duncker, 1929/1955; Wade, Swanston, Howard, Ono & Shen, 1991) and collinear induced motion (Loomis & Nakayama, 1973; Tynan & Sekuler, 1975). No published study to date has investigated its directional tuning properties, i.e. its magnitude across a number of test-inducer direction separations. This is a significant omission since doing so should provide clear evidence of whether the phenomenon can in fact be attributed to differential processing. Induced motion can be equated with the underestimation of the inducer speed (Rock et al., 1980). Therefore, if the inducer speed is kept constant, the size of the induced motion component should also remain constant across different test-inducer direction separations. Thus, for all direction separations, we should be able to predict the size of shifts in the perceived test direction by vectorially summing the constant induced motion component with the veridical test velocity.

The common practice of measuring induced motion with orthogonal inducer and test stimuli may not yield the largest effect and is in fact an arbitrary choice of measurement. The differential processing account contends that the largest shifts will occur at much smaller test-inducer separations simply due to geometrical constraints.

The differential processing hypothesis also makes certain predictions regarding the effects of the relative test and inducer speeds. Up to a certain speed (remembering that induced motion is

speed-tuned), the greater the inducer speed the greater the induced motion in the test stimulus should be. According to the hypothesis, the trajectory of the test stimulus is a vector sum of its veridical and induced motion components. If the inducer speed is increased relative to the test speed, the induced motion component will increase with respect to the veridical component. The result will be a larger shift in the perceived test direction. Conversely, decreasing the relative speed will result in a smaller directional shift. It is therefore predicted that the inducer-to-test speed ratio rather than the overall speed will be a significant determinant of direction shift. Further, with greater inducer-to-test speed ratios, due to the geometrical constraints of the vector summation, the peak effect should occur at smaller direction separations. Finally, the differential processing account contends that NOR speed is underestimated with respect to OR speed by a constant proportion. If this contention is true, then since induced motion supposedly arises from this relationship, it should show a constant proportional relationship to the inducing speed. These predictions are tested in the following study.

Past studies have used the nulling method to determine effect size (e.g. Zivotofsky, 2004). We have identified a serious problem with this method since the task requires participants to alter the trajectory of the test stimulus while the inducing stimulus remains unaltered. Consequently, the inducer-test direction separation is no longer at the specified direction separation. This problem is avoided in the following experiments simply by maintaining a constant inducer-test direction separation.

2.1 Manuscript 1

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Studies of the angular function of a Duncker-type induced motion illusion

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Abstract

Duncker (1929/1955) demonstrated a laboratory version of induced motion (IM). He showed that when a stationary spot of light in a dark laboratory is enclosed in an oscillating rectangular frame that the frame is perceived as stationary and the dot appears to move in the direction opposite the true motion of the frame. Zivotofsky (2004) studied a more complex variant of the Duncker illusion, in which both the inducing and the test stimuli moved: a single red test dot moved horizontally left or right while a dense background set of black dots on a white background moved vertically up or down. When the background inducing dots moved up (down), the truly horizontally translating test dot appeared to drift at an angle down (up) from the horizontal. In Experiment 1, we used two methods to measure the complete angular function of the Zivotofsky effect and found it to peak with an inducer-test direction separation of approximately 30° , similar to the inducing angle that has been found to maximise other direction illusions. Experiment 2 tested and confirmed predictions regarding the effects of relative test and inducer speeds based on the vectorial subtraction of the inducing velocity from the test velocity.

1 Introduction

A common occurrence of illusory induced motion (IM) occurs when the moon is seen through drifting clouds: the illusory percept is that the clouds are stationary and the moon is drifting in the direction opposite to the true cloud movement. Wade and Swanston (1987, p.555) quoted Porterfield (1759) as an early observer of this phenomenon:

"If two or more Objects move with the same Velocity, and a third remain at rest, the Moveables will appear fixed, and the Quiescent in Motion the contrary Way. Thus, Clouds moving very swiftly, their Parts seem to preserve their Situation, and the Moon to move the contrary Way."

Reinhardt-Rutland (1988) published a comprehensive review of research on IM.

Duncker (1929/1955) first demonstrated a laboratory version of IM. He showed that a stationary spot or point of light surrounded by a luminous moving frame will appear to move in a direction opposite to that of the physical motion of the frame. In addition, if the frame's motion is below the subject-relative motion detection threshold, the frame also appears stationary. In order to produce IM it is not necessary that the inducing object surrounds the test object. For example, induced motion can also be demonstrated when the test and inducing objects both are spots of light (Day et al 1979; Duncker 1929/1955; Mack et al 1975). In this case either or both spots may appear to move even though only one spot is actually moving.

Zivotofsky (2004) studied what he called a more complex variant of the Duncker illusion, in which both the inducing and the test stimuli moved: a single red test dot moved horizontally left or right while a dense background set of black dots on a white background (50% density) moved vertically up or down. The illusion was such that when the background inducing dots moved up (down), the truly horizontally translating test dot appeared to drift at an angle down (up) from the horizontal. There were large individual differences between the seven observers but

the illusions obtained were often extremely large, ranging from about 5° to greater than 80° , with several observers exhibiting illusions close to 40° and an overall mean illusion across all conditions of about 26° . In a control condition when the background inducing dots were stationary, illusory errors were negligible, averaging 2.3° .

Zivotofsky's stimuli were presented on a $20^\circ \times 20^\circ$ area of a back-projection screen and he suggested that the large illusions he obtained were due to the observers' tendency to attribute the background motion to eye movements pursuing the target, just as in the real world when a moving target is pursued, the motion of the background on the retina is not attributed to motion of the background itself. Zivotofsky's findings confirmed earlier results to which he did not refer (Gogel 1979).

Gogel (1979) showed that the real motion of a target dot (say vertical) and IM induced by a drifting background (say horizontal) sum. Thus, the phenomenal target trajectory is a vector sum of its physical motion and illusory IM induced by the drifting background. The target's perceived direction of motion is diagonal. Figure 1, adapted from Gogel (1979), illustrates this. In Figure 1, a spot (s) moves vertically (v) but is enclosed in a frame moving left. The frame induces horizontal rightward motion (h) in the spot. The resulting vector sum percept of v and h is m.

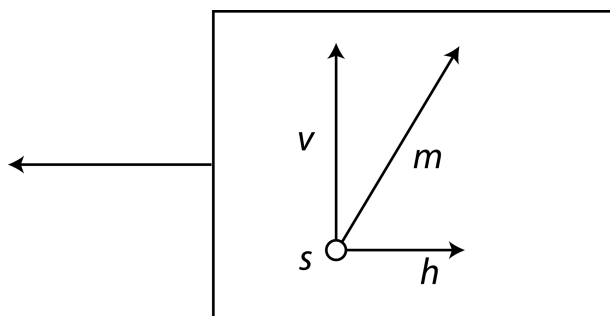


Figure 1. Adapted from Gogel (1979). Here, a spot (s) moves vertically (v) but is enclosed in a frame moving left. The frame induces horizontal motion (h) in the spot. The resulting vector sum percept of v and h is m.

There is, however, one critical difference between the methods of measurement of the perceived spot path used by Gogel and by Zivotofsky. Gogel had observers set two posts to indicate the apparent horizontal distance (h) moved by the truly vertically moving spot (v) that had no physical horizontal component at all; and he had them rotate a rod to indicate the apparent direction of motion of the spot. Zivotofsky used a staircase procedure (e.g. Wetherill and Levitt 1965) to null the illusory diagonal trajectory of the target. That is, the physical direction of the target was altered until the observer perceived the target to be moving horizontally. Such a nulling method was also used to measure IM by Levi and Schor (1984).

Because the illusory effects are very large using the Zivotofsky-type display there is a fundamental flaw in Zivotofsky's methodology. When nulling methods are used with small tilt aftereffects (say 2°) it may not much matter that a fixed inducer at, say, 15° is actually only 15° minus $2^\circ = 13^\circ$ away from the test when the aftereffect has been nulled but with very large effects it matters a lot. For example, in the case of Zivotofsky's observer who had an illusory direction shift of more than 80° , when the illusion was nulled the actual angle between the target and inducing direction would no longer have been 90° but less than 10° , i.e. 90° minus 80° .

Zivotofsky used only orthogonal inducing and test stimuli. We wished to measure the complete angular function of illusions induced by a Zivotofsky-type display, that is, the magnitude of the illusory direction shift as a function of the angular separation of inducing and test directions. Studies of direction repulsion illusions have commonly used transparent motion stimuli (superimposed random dot kinematograms or RDKs) with the finding that the perceived direction of the test RDK (arbitrarily defined as one of the two superimposed RDKs) is shifted between 10° and 20° away from the inducing direction (arbitrarily defined as the other RDK) and that the angular function shows a peak effect between about 20° and 40° inducer-test direction separation (Marshak and Sekuler 1979; Rauber and Treue 1999; Wiese and Wenderoth 2007). It would be

consistent with the hypothesis that the IM display used by Zivotofsky belongs to the same class of direction repulsion illusions as these if the Zivotofsky effect also exhibited peak effects at 20° to 40° angular separation between test target direction and inducer direction. To establish the angular separation between test and inducer directions at which the peak effect occurs was the first aim of Experiment 1.

The second aim of Experiment 1 was to measure the angular function of the direction shift in two ways using staircases. First, to repeat Zivotofsky's nulling method with the motion direction of the inducer fixed so that the test-inducer direction difference varied depending on the magnitude of the direction shift. Second, we yoked the inducer direction to the test direction so that the test-inducer angle remained constant. It was predicted that the two angular functions would peak at different *nominal* test-inducer angles. It was also predicted if the first function were replotted using the *true inducing angle* (nominal angle minus illusory direction shift) it would coincide with the second function.

2 Experiment 1

2.1 Method

2.1.1. Apparatus VPixx v2.3 software (VPixx Technologies Inc., Longueuil, Canada, www.vpixx.com) generated all stimuli and recorded all responses in an Excel file using a G5 Macintosh Dual 2 GHz Power PC running Mac OS X version 10.4.11. The SONY Trinitron Multiscan G520 monitor had a frame refresh rate of 75 Hz and a pixel resolution of 1152x870. Subjects viewed the screen binocularly from a distance of 57cm through a circular viewing tube (length 57cm, diameter 33cm) that was lined internally with matte black felt and that masked the edges of the monitor. A chinstrap and headrest prevented head movement. Left and right arrow

keys on a standard Apple keyboard were used to indicate that the red dot was perceived to be drifting left or right of vertical.

2.1.2 Subjects There were 15 subjects from an introductory Psychology course who volunteered in return for modest course credit. All were emmetropic or wore their usual corrective lenses.

2.1.3 Stimuli A random pattern of 0.18 deg visual angle white inducing dots (1 dot/deg²) on a black background drifted at a speed of 3 deg/s at angles of 0° (vertical), ±7.5°, ±15°, ±22.5°, ±30°, ±37.5°, 45°, ±60°, ±90° or ±120°. Michelson contrast, defined as $[L_{\text{MAX}} - L_{\text{MIN}}]/[L_{\text{MAX}} + L_{\text{MIN}}]$ was 0.98. In all of these inducing conditions, a 0.6 deg red test dot, when drifting physically vertical, drifted at 3 deg/s from 5 deg below the centre of the screen to the top screen centre. As the test trajectory changed, the starting position of the dot followed an arc with a radius of 5 deg from the screen's centre so that it always passed through the centre of the screen. The circular viewing tube masked the display edges to remove all cues to true vertical and horizontal. The circular inducing dot field subtended 33 deg. Stimuli were presented for a maximum of 1s but subjects were instructed to respond as soon as they felt able to make a decision as to whether the red dot appeared to be drifting left or right of vertical. If no response had been registered before stimulus offset, a grey background was presented until a response was registered.

There were two reasons for using a short 1s presentation. First, the task was very easy so that 1s was ample time to make the judgment. Second, subjects were specifically instructed to respond to the initial perceived direction of motion of the test dot, because the authors had observed that its path often appeared to curve with long exposure durations. This curvature was towards true vertical, opposite that reported previously (Post and Chaderjian 1988). In our case we think this occurred because as the dot nears the top of the aperture with a long exposure there

are increasingly obvious cues to the fact that the dot is still in the centre of the screen, with positional cues thus countering the illusory shift in direction away from true vertical.

There was no fixation point and free inspection was permitted because Zivotofsky (2004) found that when he used presentation times of 200 ms and 50 ms, 4 of his 6 observers obtained non-significantly different effects at the two exposure durations and 2 obtained significantly *larger* effects at the shorter duration that was too brief for target tracking to occur. Zivotofsky (2004) concluded: "Our data with the 50-ms exposure rule out any role of eye movements in generating the illusion" (p. 2870).

2.1.4 Procedure For each inducing angle, a single staircase procedure was used to measure the point of subjective vertical motion of the test dot. Whenever the observer pressed the left arrow key to indicate perceived test stimulus motion left of vertical, the staircase procedure moved the test trajectory to the right, and vice versa. Pilot studies indicated that most direction shifts were so large that it was adequate to begin each staircase with the red dot moving in the true vertical direction. Step sizes for each reversal were 10, 5, 4, 3, 2, and 1° thereafter. Each condition was terminated after 10 reversals, with the mean of the final 8 reversals from each staircase averaged to give the estimated point of subjective vertical motion (PSVM).

Measurements were counterbalanced with an equal number of trials conducted with a clockwise (CW) oriented inducing display and a counterclockwise (CCW) oriented inducing display. Because there were so many inducing angles, the one-hour testing session was divided into 6 blocks of staircases with a 2-minute break between blocks. The 6 blocks were as follows. Blocks 1-3 used inducing angles that were fixed (as Zivotofsky had done) so that a nominal inducing angle of θ° was truly θ° only when the test dot was actually drifting vertically. Otherwise, the actual inducing angle was the nominal fixed angle minus the illusory direction

shift. Blocks 4-6 used test-relative inducing angles so that the inducer was at a variable absolute angle that always kept the angle between the test and inducing direction at θ° . For example, in Blocks 1-3, when the inducing angle was horizontal right (90°) and the test angle was vertical (0°), the inducing minus test angle was 90° minus $0^\circ = 90^\circ$. But if the staircase procedure changed the test angle to, say, 60° then the inducing minus test angle reduced to only 90° minus $60^\circ = 30^\circ$ because the inducing angle was fixed at 90° . In Blocks 4-6, however, if the test angle became 60° the inducing angle changed from 90° to 90° plus $60^\circ = 150^\circ$ so that the inducing minus test angle was always maintained at 90° .

Each subject completed the 6 blocks in a different random order. Inducing angles were: in blocks 1 and 4, $\pm 0^\circ$, $\pm 15^\circ$, $\pm 45^\circ$ and $\pm 90^\circ$; in blocks 2 and 5, $\pm 7.5^\circ$, $\pm 22.5^\circ$ and 37.5° ; and in blocks 3 and 6, $\pm 30^\circ$, $\pm 60^\circ$ and $\pm 120^\circ$. Within each block, the 6 (blocks 2, 3, 5 and 6) or 8 (blocks 1 and 2) inducing orientations were randomly interleaved.

Prior to the start of the experiment, subjects were given brief practice trials with fixed inducing angles only of $\pm 0^\circ$, $\pm 45^\circ$ and $\pm 90^\circ$ ($\pm 0^\circ$ simply means that this condition was repeated). As in the experiment to follow, the 6 practice staircases were randomly interleaved and terminated after 6 reversals.

2.2 Results

PSVMs for CW and CCW inducing trials were combined and reported as single values measured in degrees CCW of vertical, as if all conditions incorporated an Inducing direction CW of the Test direction. Since CW and CCW measurements were counterbalanced, no baseline adjustments (pretests) were necessary. The means and standard errors of the illusory direction shifts obtained are shown in Figure 2.

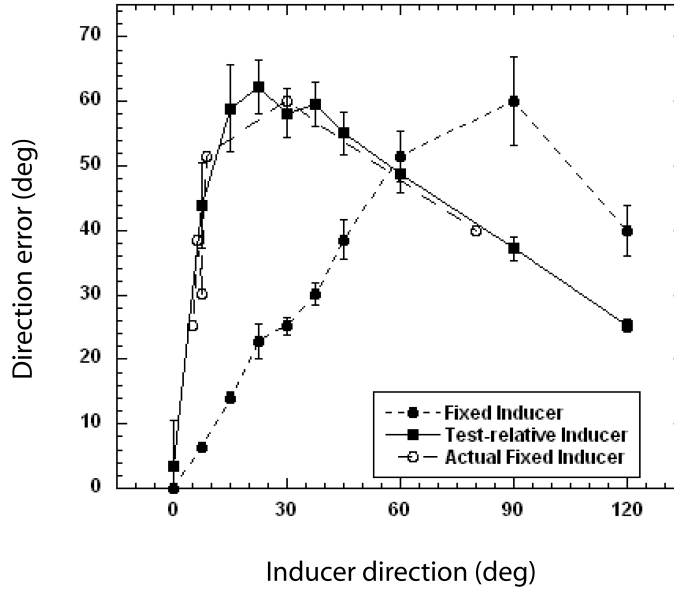


Figure 2. Means and standard errors of PSVMs (illusory direction shifts). Inducing direction 0° = vertical, 90° = horizontal. Fixed inducer refers to conditions in which the inducing direction was always the direction shown on the abscissa, regardless of the motion direction of the test dot. Test-relative inducer refers to conditions in which the inducing direction varied with the direction of the test dot to keep the angle between test direction and inducing direction constant and equal to that shown on the abscissa. Actual fixed inducer plots the fixed inducer illusions but at the real inducing angle, namely nominal inducing angle shown on the abscissa minus the PSVM or illusory direction shift.

Two examples of the data shown in Figure 2 can be used to explicate the data plotted as "Actual Fixed Inducer". For a Fixed Inducer of 90° , the direction shift is 60.07° . This means that the red dot appeared to move vertically when actually moving 60.07° CW. Because the Fixed Inducer was still drifting horizontally at 90° , the true angle between the test and inducing directions was $(90 - 60.07) = 29.93^\circ$. Hence in the Actual Fixed Inducer data the illusion of 60.07° is plotted above 29.93° on the abscissa. In the case of the fixed 30° inducer the direction shift was 25.15° . This means that the actual angle between the test and inducer directions when the test appeared to drift vertically was $(30 - 25.15) = 4.85^\circ$. So in the Actual Fixed Inducer data the direction shift of 25.15° is replotted above the direction 4.85° on the abscissa.

2.3 Discussion

Experiment 1 was designed to measure the complete angular function of the illusory direction shift in two ways using staircases. First, we repeated Zivotofsky's (2004) nulling method with the motion direction of the inducer fixed so that the test-inducer direction difference varied depending on the magnitude of the direction shift. Second, we yoked the inducer direction to the test direction so that the test-inducer angle remained constant regardless of the test dot's direction. It was predicted that the two functions would peak at different *nominal* test-inducer angles but that if the first function were replotted using the *true inducing angle* (i.e. nominal inducing direction minus direction shift magnitude) it then would be coincident with the second function. Clearly, Figure 2 very strongly supports that reasoning and, in our view, validates the method of yoking the inducing motion direction to the direction of the test dot.

In the introduction, we noted that if the IM display used by Zivotofsky belongs to the same class of direction repulsion illusions reported by Marshak and Sekuler (1979), Rauber and Treue (1999) and Wiese and Wenderoth (2007), then it too might be expected to exhibit peak effects at 20° to 40° angular separations between test target and inducer direction separations (see the last two paragraphs of the Introduction).

Figure 2 shows that in the Fixed Inducer condition the illusory direction shift *appears* to exhibit a peak effect at a test-inducer motion direction difference of 90°. However, when this angular function is replotted using the Real Fixed Inducer calculation it exhibits a peak illusion of 60.07° at 29.93°, very close to 30°. Consistent with this, the angular function of the illusion in the Test-relative Inducer condition peaks between 15° and 37.5° test-inducer direction difference with illusions at 15°, 22.5°, 30° and 37.5°, respectively, of 58.9°, 62.3°, 58.1° and 59.6°.

3 Towards a model of IM

As we have seen, Gogel's (1979) model is based on the principle that IM and physical motion can be vectorially summed. If this is true, then, as depicted in Figure 3, IM must result from a perceptual change in the speed of the motion component that is parallel to the inducer (x), while the motion component that is orthogonal to the inducer (y) will remain unchanged.

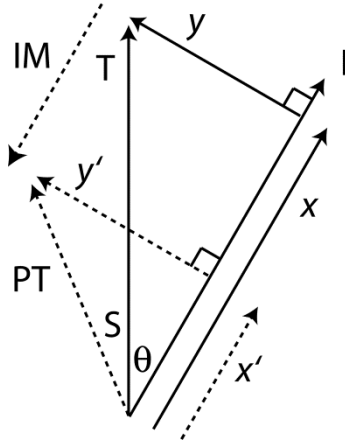


Figure 3. Vector diagram used to calculate the magnitude of IM. Actual motion vectors are represented by solid arrows and perceptual vectors by dashed arrows. The test velocity (T) is vertical. θ is the directional separation of test and inducer, so the inducing velocity (I) has a direction θ° CW of vertical. S is the shift in the perceived direction of the test, so the perceived test velocity (PT) has a direction S° CCW of vertical. The test velocity is broken down into two component velocities, that which is parallel to the inducer (the x -component) and that which is orthogonal to the inducer (the y -component). The perceived test velocity is also broken down into parallel (x') and orthogonal (y') components. The induced motion (IM) is opposite the inducing direction, and can be calculated as the difference between x and x' .

In Experiment 1, our independent variable was the test-inducer direction difference, θ , and the speed of both test (T) and inducer (I) was fixed at 3 deg/s. In addition, the component velocities, x and y , were known quantities: $y = 3.\sin(\theta)$ and $x = 3.\cos(\theta)$. For each value of θ , we obtained a value for our dependent variable, the shift in perceived direction, S . To obtain a measurement of IM, we first calculated the value of the perceptual speed of the x -component (x') and subtracted this from its actual speed (x). We found the mean IM value across test-inducer differences (θ) to range from 2.272 deg/s when $\theta = 120^\circ$ to 2.650 deg/s when $\theta = 22.5^\circ$. A set of

one-sample two-tailed t-tests found the effect to be significantly different from zero for all measured inducer directions ($t_{(14)} \geq 15.559$, $p < 0.0005$, $\eta^2 = 0.945$). A one-way repeated measures ANOVA found the main effect of direction difference to be small but significant ($F_{(8,112)} = 3.402$, $p = 0.002$). Pairwise comparisons found significant differences between the $\theta = 22.5^\circ$ and $\theta = 90^\circ$ conditions ($p = 0.020$), between the $\theta = 37.5^\circ$ and $\theta = 90^\circ$ conditions ($p = 0.012$), and between the $\theta = 37.5^\circ$ and $\theta = 120^\circ$ conditions ($p = 0.044$) only (p -values were Bonferroni-adjusted to control for overall error rate). Although the main effect of direction difference was significant, because it was so small we considered ourselves justified in calculating the IM averaged across direction differences: $IM = 2.488 \text{ deg/s}$ ($SE = 0.105$).

If the perceived test direction (PT) results from a vector sum of IM and the actual test direction (T), we should be able to predict to a very close approximation the results of Experiment 1 with our single obtained value of IM. These predictions are presented in the graph in Figure 4, which shows predicted values that very closely resemble the data obtained in Experiment 1 (yoked inducer data replotted from Figure 2). The results obtained in Experiment 1 can therefore be summarised almost entirely by the vectorial model $PT = T - IM$.

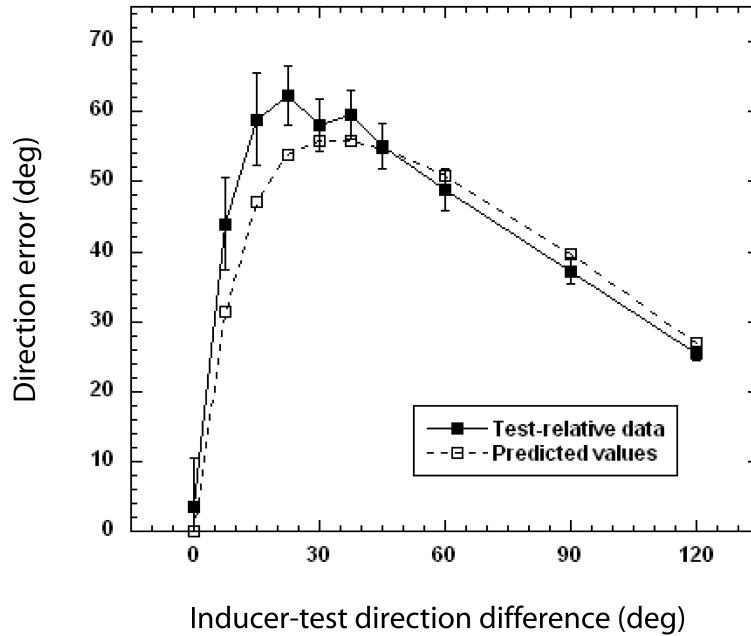


Figure 4. The shift in perceived test direction across inducer-test direction differences as obtained in Experiment 1 using the yoked inducing direction (solid plot) and as predicted by the model $PT = T - IM$ (dashed plot). Shifts were calculated from a single IM value of 2.488 deg/s.

4 Experiment 2

The aims of this experiment were:

1. To test several predictions made by Gogel's (1979) model regarding the effects of the relative speeds of the inducing dots and the test dot on the illusory direction shift, using the yoked staircase method.
2. To establish a simple vector-subtraction model of the direction shift that can account for the effects of varying inducing and test speeds.

Two of our predictions can be derived from Figure 5. Comparing (a) and (b), the faster inducing speed in (a) results in a larger direction shift because the perceived trajectory of the test dot in (a)

is further from the true vertical direction than it is in (b). That is, $(90^\circ \text{ minus } \alpha) > (90^\circ \text{ minus } \beta)$.

So the first prediction was that

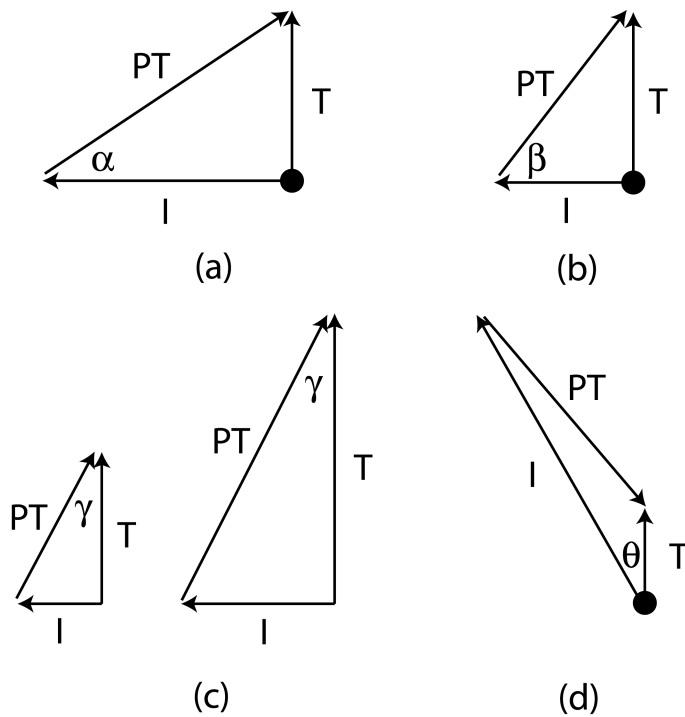


Figure 5. In all vector diagrams T is the true test dot direction and speed, I is the inducing direction and speed and PT is the perceived test dot trajectory.

systematically increasing inducing speed would systematically increase the magnitude of the illusory direction shift. Zivotofsky (2004) reported some relevant evidence but he did not vary inducing speed systematically. Rather he ran one condition in which test and inducer speeds were both 20 deg/s and another in which inducer speed remained at 20 deg/s but test speed was increased to 40 deg/s. He reported (p.2870) that the illusion was 56% weaker in the latter condition. Figure 5(c) shows that when the ratio between the test and inducing speeds is held constant, in this example 1.37:1, the angle (λ) between true vertical and PT – the illusory direction shift – should be constant. This was the second prediction tested in Experiment 2. When we later present the results of Experiment 2, it will be seen that there are no data points for

inducer speeds of 6.25 deg/s and 7.5 deg/s at inducer-test direction differences of 30° and 60°. The reason can be explained using figure 5(d). When the test-to-inducer speed ratio is very small and the inducer-test direction separation is small the test dot is perceived to be drifting down. Because pilot subjects found this confusing we decided not to run those conditions.

A third prediction can be derived from Figure 3. The two methods of measuring IM described in Experiment 1, one with a fixed inducer and the other with a yoked inducer, produced respective peaks in direction shift (S) at $\theta = 90^\circ$ and $\theta = \sim 30^\circ$. In the former case, the results are reported as a function of the *perceived* angular separation ($\theta + S$) of test and inducer. In fact, such results *must* show a peak at $\theta + S = 90^\circ$ because it is geometrically determined. Consider the trigonometric identity: $IM/\sin(S) = T/\sin(\theta+S)$. From this identity, we can formulate the following equation:

$$\text{Equation 1: } S = \sin^{-1} ((IM/T) \cdot \sin (\theta + S)) \text{ (See Figure 3).}$$

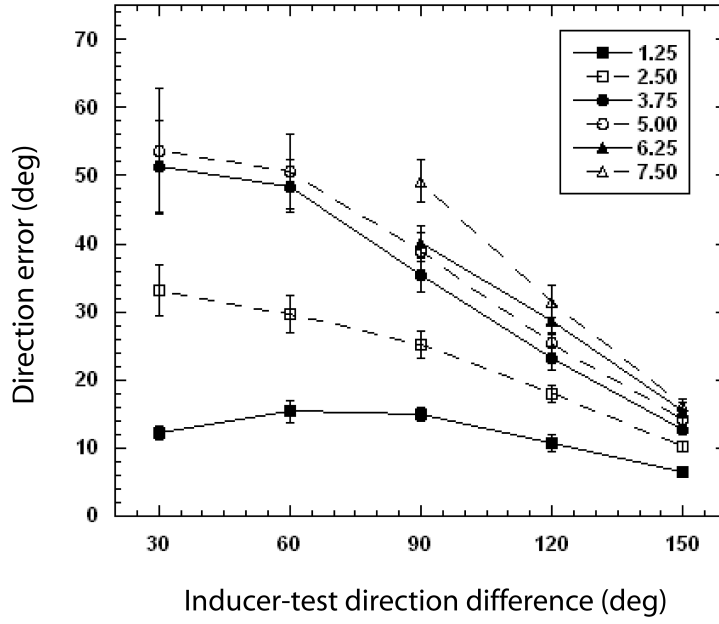
From Equation 1, we can state that for any given constant IM value, the closer to 90° the perceived directional difference between inducer and test ($\theta + S$), the larger the directional shift (S) will be. The greatest shift (S) must therefore occur when $\theta + S = 90^\circ$. We have also observed, using the yoked inducer method, that S peaks when $\theta = \sim 30^\circ$ (actually between 22.5 and 45°). It can be seen from Figure 3 and from Equation 1 that the greater the IM, the greater S will be. So, if we can increase the IM, we will also increase S. And since S is greatest when $\theta + S = 90^\circ$, S will peak at a smaller value of θ . From Experiment 1, IM was calculated to be ~ 2.5 deg/s, and S was found to peak at $\theta = \sim 30^\circ$. Therefore, if $IM > 2.5$, S should peak at $< 30^\circ$, and with increasing IM, S will peak at decreasing values of θ . Since we have predicted that IM will increase with inducer speed, S should peak at decreasing values of θ as inducer speed is increased. This was a further prediction that we wished to test in Experiment 2.

3.1 Method

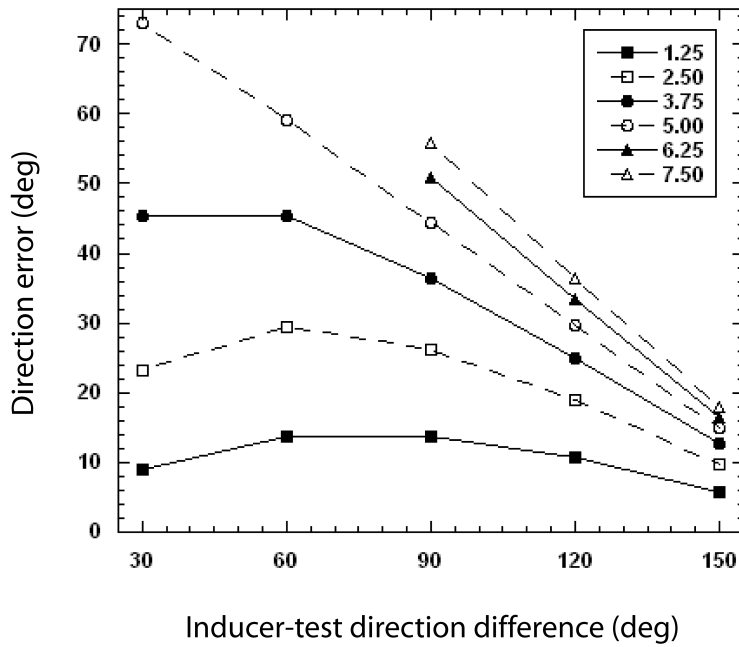
Most aspects of methods were as in Experiment 1. Differences were as follows. There were 120 conditions, 2 test dot speeds (2.5 and 5 deg/s) x 6 inducing dot speeds (1.25, 2.5, 3.75, 5, 6.25 and 7.5 deg/s) x 10 test-inducing motion direction separations ($\pm 30^\circ$, $\pm 60^\circ$, $\pm 90^\circ$, $\pm 120^\circ$ and $\pm 150^\circ$). Because the inducing stimulus parameters varied greatly in both direction and speed, potentially complicating the experimental task, we simplified the stimulus by having the trajectory of the test dot originating at the screen's centre in every trial. Further, because there were so many conditions, the single staircases were terminated after 6 reversals and the last two were averaged. Step sizes were 5° , 2° , 1° , 1° and 0.5° . There were 21 subjects drawn from the same population as those in Experiment 1.

3.2 Results

Figure 6(a) shows the means and standard errors of illusory direction shifts when test dot speed was 2.5 deg/s and Figure 7(a) shows the same for test dot speed of 5 deg/s.

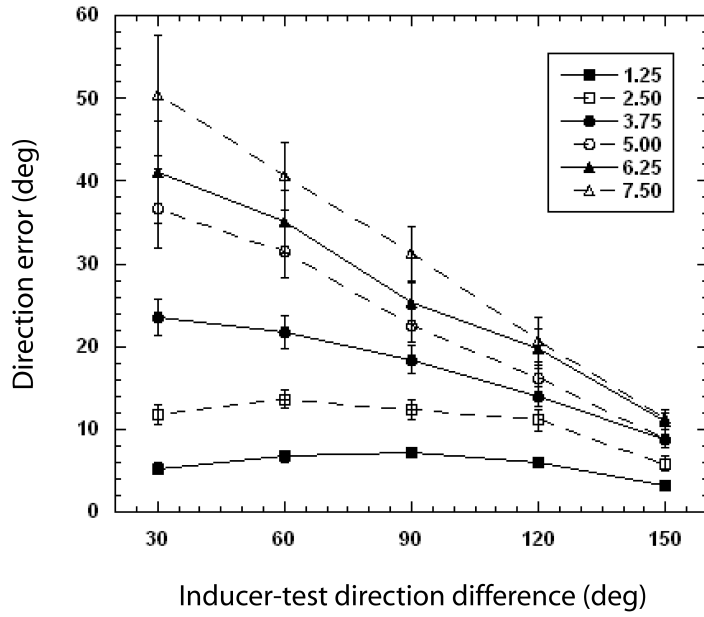


(a)

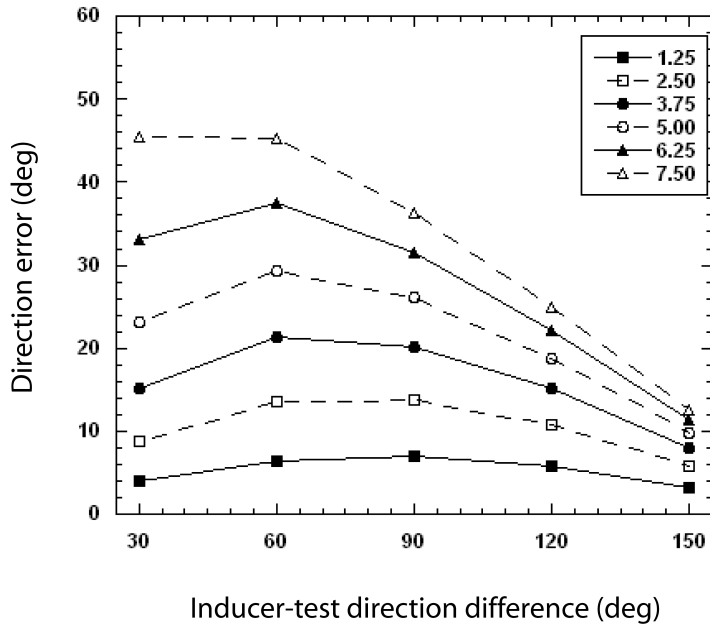


(b)

Figure 6. (a) Illusory direction shifts for the 2.5 deg/s test dot for 6 inducing speeds and 5 test-inducing direction differences (\pm direction differences averaged). (b) Illusory direction shifts for the 2.5 deg/s test dot predicted by the model $PT = T - k.I$, with the constant $k = 0.4907$.



(a)



(b)

Figure 7. (a) Illusory direction shifts for the 5 deg/s test dot for 6 inducing speeds and 5 test-inducing direction differences (\pm direction differences averaged). (b) Illusory direction shifts for the 5 deg/s test dot predicted by the model $PT = T - k \cdot I$, with the constant $k = 0.4907$.

In both Figures 6(a) and 7(a) there is a clear ordering of direction shift magnitude as a function of inducing speed, confirming our first prediction. Figure 8 replots some of the data from Figures 6(a) and 7(a) as direction errors for 2 test dot speeds and 3 test-to-inducer speed ratios as a function of inducer-test direction separation. From the figure legend it can be seen that the test-to-inducer speed ratio is 2 for the square symbols, 1 for the circular symbols and 0.66 for the triangular symbols. Our second prediction was that direction shift functions for equal test-to-inducer speed ratios would be the same. This was confirmed through a multi-factorial analysis, which showed main effects of test-to-inducer speed ratio ($F_{2,40}=103.42$, $p<0.001$) but no main effect of test speed ($F_{1,20}=1.74$, $p=0.2$). There was also a main effect of direction difference ($F_{2,80}=44.86$, $p<0.001$).

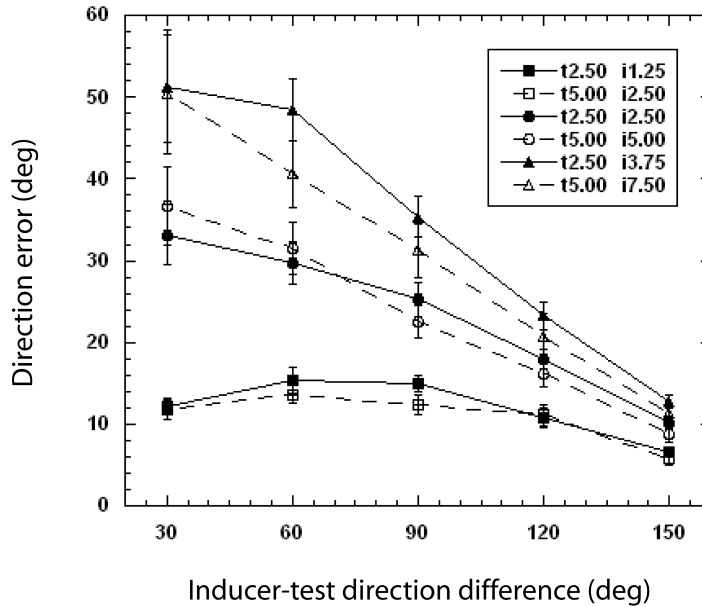


Figure 8. Some of the data from Figures 6(a) and 7(a) replotted as direction errors for 2 test (t) dot speeds and 3 test-to-inducer speed ratios (2.0, 1.0 and 0.67) as a function of inducer-test direction separation.

There was a significant interaction between test-to-inducer speed ratio and direction separation ($F_{8,160}=22.67$, $p<0.001$) but not between test speed and direction separation ($F_{4,80}=0.73$, $p=0.58$) or between test speed and test-to-inducer speed ratio ($F_{2,40}=2.40$, $p\leq 0.10$).

Our third prediction was that the peak shift in perceived direction would occur at smaller inducer-test directional differences as the test-to-inducer speed ratio was decreased. This was also confirmed by our results. In Figures 6(a), 7(a) and 8, the higher test-to-inducer speed ratios produced peaks in direction shift S at direction differences of $\theta \approx 90^\circ$, and the peak in S appears to occur closer to $\theta = 0^\circ$ as the ratio is decreased.

5 Modelling

In Experiment 1, we found that the results could be summarised by the model $PT = T - IM$. After measuring the shift in perceived direction across a range of inducing and test speeds, we have found that increasing the inducing speed increases IM . However, we found that our results could be very closely described by the model: $PT = T - k \cdot I$, where k is a constant and represents the ratio of IM to inducer speed.

Because the experimental design was not orthogonal, remembering that we omitted conditions with small test-to-inducer speed ratios and small direction differences from our experiment (see the introduction to Experiment 2), we ran three separate analyses on our data¹.

For our first analysis, we conducted a 2 (test speed) x 4 (inducer speed) x 5 (inducer-test direction separation) repeated measures ANOVA. We ran the analysis on only 4 inducer speeds (1.25, 2.5, 3.75, and 5 deg/s), since the other two inducing speeds (6.25 and 7.5 deg/s) were not

¹ The data obtained from one observer were omitted because in one condition (test speed = 5 deg/s, inducer speed = 7.5 deg/s, direction separation = 120°) he/she produced an IM value of 121.52. The mean IM value for this condition was 8.452, and the standard deviation was 25.976. With the omission of that observer's data, the mean dropped to 2.798 and the standard deviation to 1.931.

tested with the 2.5 deg/s test speed at direction separations of 30 or 60°. We found that the mean IM-to-inducer speed ratio (k) averaged across inducer speeds and direction separations was 0.496 deg/s (SE = 0.034) when the test speed was 2.5 deg/s and 0.486 deg/s (SE = 0.037) when the test speed was 5 deg/s. Our multi-factorial analysis showed the main effect for test speed to be non-significant ($F_{(1,19)} = 0.308$, $p = 0.585$). Combining the data from the two test speeds produced a mean IM-to-inducer speed ratio of $k = 0.491$ (SE = 0.034). There was, however, a significant interaction between direction difference and test speed ($F_{(4,76)} = 3.407$, $p = 0.013$), with the 5 deg/s test speed producing a greater IM-to-inducer speed ratio than the 2.5 deg/s test speed at a direction difference of 30° and the 2.5 deg/s test speed producing a greater IM-to-inducer speed ratio than the 5 deg/s test speed at a direction difference of 150°. The mean IM-to-inducer speed ratio averaged across test speeds and direction differences ranged from $k = 0.442$ for the 5 deg/s inducing speed to $k = 0.533$ for the 1.25 deg/s inducing speed. The main effect for inducing speed was significant ($F_{(3,57)} = 9.286$, $p < 0.0005$). The mean IM-to-inducer speed ratio averaged across test and inducer speeds ranged from $k = 0.450$ to $k = 0.555$ deg/s for the 5 direction differences. The main effect for direction difference was significant ($F_{(4,76)} = 5.372$, $p = 0.001$). In a second analysis, we ran a two-way repeated measures ANOVA on the 5 deg/s test speed across 6 inducer speeds and 5 direction differences. As with the first analysis, significant main effects were found for both inducer speed ($F_{(5,95)} = 4.678$, $p = 0.001$) and direction difference ($F_{(4,76)} = 6.684$, $p < 0.0005$). The overall mean IM-to-inducer speed ratio was $k = 0.469$ (SE = 0.038). We also ran the following analysis: 2 test speeds (2.5 and 5 deg/s), 6 inducer speeds (1.25, 2.50, 3.75, 5.00, 6.25, and 7.50 deg/s) and 3 direction differences (90, 120, and 150°). The overall mean IM-to-inducer speed ratio was $k = 0.447$ (SE = 0.034). Again, we found the main effect of test speed to be non-significant ($F_{(1,19)} = 1.611$, $p = 0.220$), and again we found the main effect of inducer speed to be

significant ($F_{(5,95)} = 11.026, p < 0.0005$); however, the main effect of direction difference did not reach significance this time ($F_{(2,38)} = 2.256, p = 0.119$).

We calculated the overall mean value of k from all of our data: $k = 0.4907$. From our model, substituting in our calculated value k , we calculated predicted values of S that could then be compared to the experimental measurements of S that made up our data (compare Figure 6(b) to Figure 6(a) and compare Figure 7(b) to Figure 7(a)). To determine how good a fit our model provided, we ran a regression analysis, the results of which are plotted in Figure 9. A regression analysis on the predicted values of S against the mean obtained values of S produced an R^2 value of 0.901. Our model therefore accounts for approximately 90% of the variance in the data means.

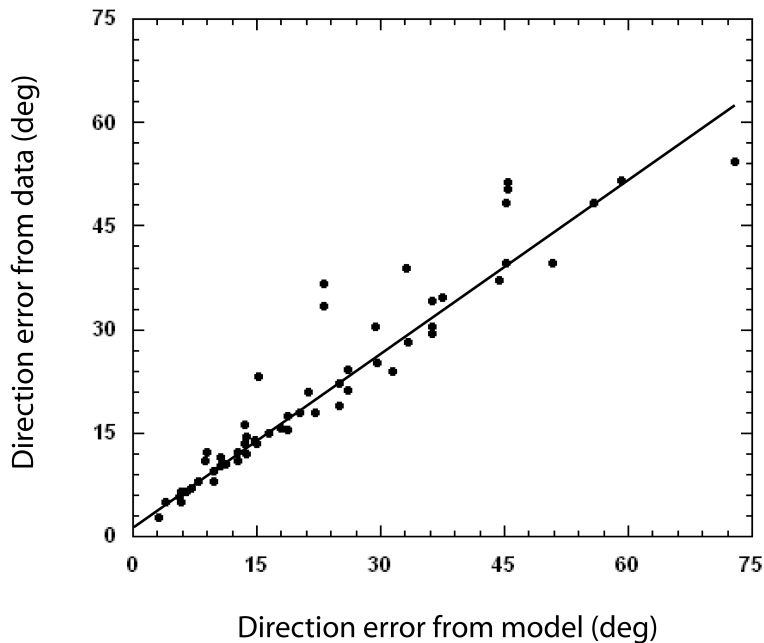


Figure 9. Means of obtained direction shifts across inducer-test direction differences (ordinate) plotted against direction shifts predicted by the model (abscissa). The regression line ($y = 2.3258 + 0.84865x$) indicates that the model $PT = T - k.I$ when $k = 0.4907$ accounts for ~90% of the variance in the data ($R^2 = 0.901$).

Since the proposed model accounted for 90% of the variance in the data means, 10% of the variance was left unexplained. This variance could quite possibly reflect a combination of

noise due to errors in direction and speed discrimination (e.g. De Bruyn and Orban 1988; Gros et al 1998; Meng and Qian 2005) and to small but significant variation of k -values across the dependent variables. Variation of k -values could be the result of known perceptual asymmetries associated with differing veridical speeds and directions of motion. For example, speed acuity has been found to be optimal for speeds of between 4 and 64 deg/s (De Bruyn and Orban 1988). There is also evidence that oblique directions are perceived less accurately than are the cardinal directions (Loffler and Orbach 2001; Rauber and Treue 1998). Further, Lott and Post (1993) have found that IM is greater when the inducer moves upward than when it moves downward.

Returning to Experiment 1, from our results we calculated the mean IM-to-inducer speed ratio to be $k = 0.829$ deg/s (SE = 0.035), which is considerably larger than our value of $k = 0.4907$ obtained in the current experiment. We suggest that the difference reflects the slight configurational change that we introduced between the two experiments. The greater effect observed in Experiment 1 may have resulted from the test stimulus originating at a point below the centre of the screen. As discussed in Section 2.1.3, as the test dot approaches the top of the screen the effect is reduced by positional cues. Alternatively, changing the test dot's starting position from trial to trial in Experiment 1 may have removed positional cues that were available in Experiment 2, resulting in observers registering greater directional errors.

6 General Discussion

Experiment 1 showed that whereas the angular function of the direction shifts due to the Zivotofsky (2004) Duncker-type illusion appeared to peak when the inducer-test separation was 90° , in fact the effect was so large that the data had to be replotted so that the X-axis showed the true inducer-test separation (Figure 2). When this was done, the peak illusion occurred between 20 - 40° inducer-test separation, similar to the angular function of the motion direction illusion and

aftereffect (see, for example, Wiese and Wenderoth, 2007). We showed that the results could be summarised by the vectorial model $PT = T - IM$, and that $IM = 2.488 \text{ deg/s}$.

Experiment 2 tested predictions derived from vector diagrams (Figure 3) that suggested that illusory direction shift magnitude would be determined by the ratio of test speed to inducer speed, with larger effects occurring when this ratio was smallest and with no effect of absolute test or inducer speed. We also tested the prediction derived from the vectorial relationships illustrated in Figure 5 that the peak shift in perceived direction would occur at smaller inducer-test directional differences as the test-to-inducer speed ratio was decreased. All of these predictions were confirmed by our results (Figures 6(a), 7(a) and 8).

While the peak effect appears to have occurred at an inducer-test separation of $\sim 30^\circ$ when the test and inducer speeds were equal, we found that the peak occurred at different inducer-test separations as the ratio of test-to-inducer speed was varied. This might at first seem incongruous with the suggestion that IM and the DI share a common mechanism. However, since no studies have yet investigated the effects of the test-to-inducer speed ratio on the angular function of the DI, we cannot discount the possibility that it too would exhibit peak effects at various inducer-test separations depending on the relative speed of the test and inducing stimuli. We therefore further conclude that there is no reason to believe that Zivotofsky's illusory direction shifts are qualitatively different from the DI and DAE. This conclusion is important because it suggests that the DI, the DAE and the Zivotofsky illusion can probably be classified as similar illusory effects and may well have a common mechanism. In the absence of the replotted data in Figure 2, the data gave the impression that whereas the DI and DAE exhibit peak effects at inducer-test separations of 20° - 40° , the Zivotofsky effect peaks at 90° inducer-test separation. This in turn could easily mislead researchers into believing that the Zivotofsky effect has a mechanism completely different from that of the DI and the DAE.

In developing a model for the effects observed in Experiments 1 and 2, we have found that the partial vector subtraction of the inducing velocity could account for nearly all of the variation in our data. This finding lends support to Gogel's (1979) vector-sum model of IM. Further, we have extended this model by showing that the vector subtraction can be calculated from the ratio of IM to inducer speed. The current findings are strongly indicative of the truth in the assumption that the observed shifts are the result of a one-dimensional induced speed shift in the opposite direction to the inducing motion. However, such a conclusion cannot be drawn with complete confidence until the perceived test speed is also measured. This will be the undertaking in a planned future study.

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3 The distribution shift and differential processing

The direction illusion (DI) is observed in bidirectional transparent motion and is generally attributed to mutual inhibition between two populations of cells, each tuned to a specific range of directions of motion. Each population displays a peak response to one of the two directions, but the mutual inhibition invoked by the simultaneous presentation of two directions causes the peak responses to shift apart. This account is referred to as the distribution-shift model. This explanation was challenged by Dakin and Mareschal (2000), who argued that the distribution-shift model fails to account for some of the observed characteristics of the illusion. Instead, they proposed the involvement of differential processing. While the distribution-shift model implies that the illusion stems from responses to two veridical velocities, the differential processing account implies that the illusion stems from responses to the NOR and OR component velocities, which have been perceptually organised into separate, orthogonal dimensions.

The following manuscript introduces an additional stimulus into the bidirectional RDK. Adding a static line that bisects the display at an orientation orthogonal to the vector average of the two motion directions allows two very different predictions to be made about the properties of the DI according to the respective models. Further, a new stimulus configuration consisting of a unidirectional RDK and a static line is found to produce a direction illusion comparable to the DI, which has here been named the statically induced direction illusion (SDI). A series of reported direction illusions ostensibly resembling the SDI show that when a motion trajectory and a static line intersect at an oblique angle, that angle will be perceptually overestimated (Cesaro & Agostini, 1998; Gogel, 1977; Khuu, 2012; Nihei, 1973, 1975; Swanston, 1984; Wenderoth & Johnson, 1983). These illusions have generally been described as motion-defined, or ‘kinetic’, analogies of various forms of the tilt illusion, e.g. the Zollner illusion and the

Poggendorff illusion, since they produce effects of similar size, i.e. approximately 2° (e.g. Swanston, 1984) and, like the tilt illusion, kinetic illusions have been attributed to a distribution shift arising from mutual inhibition between channels selective for orientation (e.g. Khuu, 2012; Khuu & Kim, 2013). However, the SDI produced in the following study was an order of magnitude larger than these illusions, although Khuu and Kim (2013) did find larger effects than the other studies, and therefore its occurrence cannot be readily attributed to a distribution shift, as will be discussed herein.

3.1 Manuscript 2

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Challenging the distribution shift: Statically-induced direction illusion implicates differential processing of object-relative and non-object-relative motion

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Abstract. The direction illusion is the phenomenal exaggeration of the angle between the drift directions, typically, of two superimposed sets of random dots. The direction illusion is commonly attributed to mutual inhibition between direction-selective cell populations (distribution-shift model). A second explanation attributes the direction illusion to the differential processing of relative and non-relative motion components (differential processing model). Our first experiment demonstrates that, as predicted by the differential processing model, a static line can invoke a misperception of direction in a single set of dots – a phenomenon we refer to as the statically-induced direction illusion. In a second experiment, we find that the orientation of a static line can also influence the size of the conventional direction illusion. A third experiment eliminates the possibility that these results can be explained by the presence of motion streaks. While the results of these experiments are in agreement with the predictions made by the differential processing model, they pose serious problems for the distribution-shift account of shifts in perceived direction.

Keywords: direction illusion; direction repulsion; transparent motion; induced motion; tilt illusion; motion streaks

1 Introduction

Our perception of the motion of an object is determined both by its spatial context and the motion of the object itself. An everyday example of the influence an object's spatial context has on its perceived motion comes from Rubin (1927), who described an observer's perception of a passenger waving with vertical hand movements from the window of a passing train. The observer does not perceive the passenger's hand tracing out a sine wave, which is its path of motion relative to the observer (veridical motion). Instead, the train becomes a perceptual frame of reference, and the hand is seen as oscillating vertically, relative to the train. Effects of spatial context on perceived motion have long been used in studies of the human visual system (e.g. Duncker, 1929/1955). One such effect, known as the direction illusion, is the phenomenal exaggeration of the angle between the respective directions of two stimuli translating in the frontoparallel plane (Marshak & Sekuler, 1979; Mather & Moulden, 1980). The direction illusion is typically observed in transparent motion displays, such as bidirectional random dot kinematograms (RDKs), which consist of two superimposed sets of random dots moving continuously, each in a different direction.

1.1 Distribution-shift model

The direction illusion is generally thought to arise from mutual inhibition between direction-selective cell populations that are most responsive to the two veridical directions in the display, as postulated by the distribution-shift model (e.g. Mather, 1980; Mather & Moulden, 1980) (Figure 1A). The distribution-shift model is based on the premise that a stimulus moving in a constant direction in the frontoparallel plane evokes responses in a population of cells tuned to a continuum of directions of motion. The activity in these cells can be represented by an approximately Gaussian distribution, with its peak indicating the responses of cells tuned

specifically to the stimulus' veridical direction, and its tapering flanks corresponding to the responses of cells tuned to increasingly divergent directions (e.g. Albright, 1984) (Figure 1B). Cells that usually respond maximally to a given direction are inhibited when a second stimulus of a different direction is presented simultaneously (see Snowden, et al., 1991). However, cells tuned to more divergent directions are less inhibited by the additional stimulus. The distributions thus become skewed, so that cells less affected by the inhibition are now the cells most responsive to the stimulus. As a result, the peaks of the two response distributions shift apart, invoking a percept of the two directions being more divergent than they actually are. Mutual inhibition thus distorts the perceived motion trajectories in a way that has been described as direction 'repulsion' (Marshak & Sekuler, 1979; Rauber & Treue, 1999; Raymond, 1993). The distribution-shift model is widely considered as applying to the domain of motion direction. However, an essentially identical model was originally introduced to account for distortions in perceived orientation, namely the tilt illusion - the phenomenal exaggeration of the angle between two differently oriented static lines (Blakemore, Carpenter, & Georgeson, 1970). Like the direction illusion, the tilt illusion has been attributed to mutual inhibition, but between orientation- rather than direction-selective cell populations (Blakemore, et al., 1970; Carpenter & Blakemore, 1973; Wenderoth, O'Connor, & Johnson, 1986).

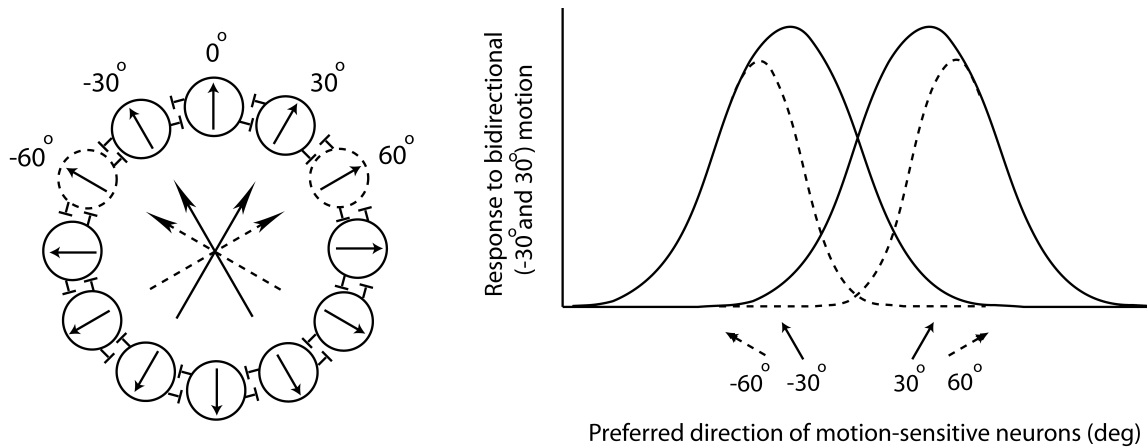


Figure 11. Diagrams explaining the direction-contrast illusion (Graham & Hochman, 1989). (A) An explanation of direction repulsion as resulting from mutual inhibition between direction-selective cell populations (adapted from Hiris & Blake, 1996). When presented with a bidirectional (e.g. $\pm 30^\circ$) stimulus (solid central arrows), cells tuned to vertical are most inhibited, since these cells are equally responsive to either direction. The cells tuned maximally to the two stimulus directions are also inhibited to an extent so that the cells tuned to more divergent directions (dashed circular outlines) are now the most responsive, resulting in a perceptual exaggeration of the difference between the two directions (dashed central arrows). (B) The hypothetical responses (not to scale) of a population of direction-selective cells to a particular stimulus can be represented by a Gaussian distribution. When two directions ($\pm 30^\circ$) are presented simultaneously, activation of cells that respond to both directions is suppressed. The distributions thus become skewed, such that cells tuned to, say, -60° are now most responsive to the -30° stimulus. Thus, the population response to a -30° stimulus now evokes a percept of a stimulus moving at -60° .

1.2 Differential processing model

Dakin and Mareschal (2000) argued that mutual inhibition between direction-selective channels does not explain certain aspects of the direction illusion, and they presented a variation of the phenomenon to demonstrate this. Two sets of dots with a direction separation of 45° would normally yield a large direction illusion (e.g. Grunewald, 2004; Marshak & Sekuler, 1979; Wiese & Wenderoth, 2007). Dakin and Mareschal found that including a third set of dots drifting at sufficient speed in a direction opposite to the vector average direction of the first two eliminated the effect. They asserted that the distribution-shift model makes no such prediction. However, there is a possible problem with discounting the distribution-shift model based on this finding alone. Although the third set was directionally distant from the other two sets ($\pm 157.5^\circ$, respectively), and although repulsion in many cases is found to persist only up to direction

separations of 120-135° (e.g. Grunewald, 2004; Marshak & Sekuler, 1979; Wiese & Wenderoth, 2007), Dakin and Mareschal (2000) themselves, in another experiment from the same paper, recorded significant repulsion with a direction separation of 135°. Moreover, we know that the greater the ratio of speeds for the two sets of dots (up to a ratio of ~2:1), the greater the shift in the slower set (Benton & Curran, 2003; Dakin & Mareschal, 2000; Kim & Wilson, 1996; Lindsey, 2001; Marshak & Sekuler, 1979). Hence, the possibility remains that, through mutual inhibition, the third set of dots was invoking counteractive angular repulsion on each of the other sets to cancel out the initial direction illusion. Notwithstanding this possibility, Dakin and Mareschal (2000) suggested that the phenomenon could be more adequately explained in terms of an alternative model. They proposed that the direction illusion results instead from the differential processing of two types of relative motion, similar to that described by Johansson (1950). Johansson (1950) contended that the veridical velocity of an object is perceptually broken down into two component velocities: an object-relative component and a non-object-relative component. He described the object-relative component as the motion that is ‘unique’ to the object and the non-object-relative component as that which is ‘common’ to all objects in the visual field with respect only to the observer. Returning to Rubin’s example, the veridical sinusoidal motion of the waving hand is parsed into object-relative and non-object-relative components, being respectively its vertical motion relative to the train and the horizontal motion common to both the train and the hand. Johansson further asserted that the non-object-relative component velocity provides a reference frame for the object-relative component velocity of each object. Accordingly, the hand in Rubin’s example is perceived as oscillating vertically. Johansson demonstrated that this object-relative component is the ‘dominant’ percept, so that, for example, when two objects seen against a homogeneous background move at equal speed in orthogonal directions from a common point, they are perceived as moving directly away from each other.

Orthogonal to this, the non-object-relative component is also detected but is perceptually ‘secondary in character’ and not always apparent (Johansson, 1950). According to Dakin and Mareschal (2000), differential processing can potentially account for the direction illusion in much the same way: if the non-object-relative component velocity is perceptually underestimated with respect to that of the object-relative component, the directional separation of the two sets of dots in a bidirectional RDK will be perceptually exaggerated (Figure 2).

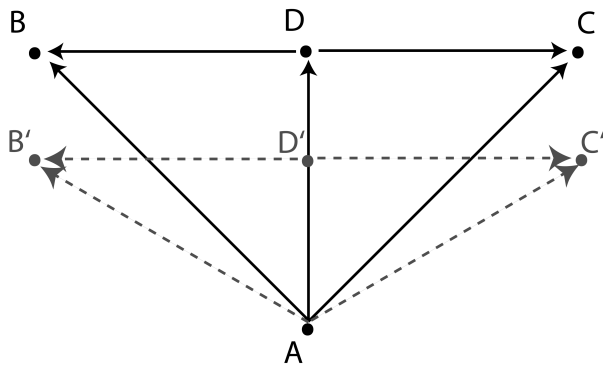


Figure 2. Vector diagram of the differential processing account of the direction illusion. Vectors AB and AC represent the veridical trajectories of two sets of dots. The non-object-relative component AD is, with respect to the object-relative component velocities D'B' and D'C', perceptually underestimated, as AD'. This results in a perceptual exaggeration of $\angle BAC$ as $\angle B'AC'$ (adapted from Dakin & Mareschal, 2000).

1.3 Supporting evidence for differential processing

Johansson's work is descriptive rather than explanatory. However, empirical justification for postulating the differential processing model comes from numerous psychophysical studies showing that separate neural processes facilitate the extraction of object-relative and non-object-relative component velocities, and that our visual system is more responsive to object-relative than to non-object-relative motion. Velocity and displacement detection thresholds (Beardsley & Vaina, 2008; Lappin, Donnelly, & Kojima, 2001; Legge & Campbell, 1981; Leibowitz, 1955; Mack, Fisher, & Fendrich, 1975; Shioiri, et al., 2002; Snowden, 1992; Sokolov & Pavlova, 2006) and reaction times (Smeets & Brenner, 1994), for example, are lower for object-relative than for

non-object-relative motion perception. Changes in stimulus luminance contrast have been found to differentially affect detection of object-relative and non-object-relative velocities. Grossman and Blake (1999) used an RDK to investigate the effects of low and high luminance conditions on object-relative and non-object-relative motion. Detection of object-relative motion required detection of a region within the RDK defined by the offset trajectories of a number of dots as they moved over the area. They found that while low luminance levels impaired the detection of object-relative motion, they did not diminish detection of non-object-relative motion. In another study, Levinson, Coyne and Gross (1980) found that when contrast was reduced to peri-threshold levels, a bi-directional RDK with an angular separation of 30° was seen as a single sheet of dots moving in a direction midway between the two component directions. The reported percept therefore corresponded with observers perceiving the non-object-relative component motion only, showing again that object-relative and non-object-relative motion perception are differentially affected by changes in contrast. Moreover, the speed of a stimulus in non-object-relative motion has been found to be perceptually underestimated in comparison to one viewed in object-relative motion (Blakemore & Snowden, 2000; Brown, 1931; De Bruyn & Orban, 1999; Gogel & McNulty, 1983; Nguyen-Tri & Faubert, 2007; Norman, et al., 1996). Brown (1931) compared the perceived velocity of dots moving against a homogeneous background with dots moving against a textured background and found the latter to appear 25% faster. Gogel and McNulty (1983) found increases of up to 42% in the perceived speed of a translating spot of light as the density of reference cues was increased from 0.1 to .65 marks/cm. Similar results have been reported in a subsequent study (Ornan, 2009). Norman, Norman, Todd, and Lindsey (1996) found that the perceived speed of a central region of random dots was higher in the presence of a surrounding region of stationary dots than when the stationary dots were absent. Blakemore and Snowden (2000) found that a dot moving across a high-contrast background appears faster than a

dot moving across a low-contrast background. De Bruyn and Orban (1999) compared the perceived speed of a set of dots when presented alone and when in transparent motion with a second set of dots moving in the opposite direction. The perceived speed was found to be 50% greater in the transparent motion condition. All of these studies indicate that objects viewed in object-relative motion are perceived as being faster than objects of equal veridical speed viewed in non-object-relative motion. Taken together, the results from the above studies constitute ample justification for considering the differential processing of object-relative and non-object-relative component velocities as a possible mechanism underlying the contextual determination of perceived stimulus direction, as in the case of the direction illusion.

1.4 Current objectives

The aim of the current paper was to evaluate and compare the adequacy of both the distribution-shift and differential processing models in accounting for the perception of stimulus direction. To this end, taking a similar approach to Dakin and Mareschal (2000), we presented new variations of the conventional direction illusion-invoking stimulus configuration that allowed distinct predictions to be made by each model. Specifically, we investigated the effects of a static line stimulus on the perceived direction of a unidirectional set of dots (Experiment 1), as well as on the perceived direction of one of the sets of dots in a bidirectional direction illusion-invoking display (Experiment 2). We also investigated whether a more broadly defined distribution-shift model might account for the results (Experiment 3).

2 Experiment 1

When the endpoints of a moving line are obscured, such as when it is viewed through a circular aperture, the line will appear to move in a direction orthogonal to its orientation, since the endpoints provide the only cue to any motion of the line parallel to its orientation. This is the

well-known ‘aperture problem’ (Wallach, 1935). The same effect can be achieved without the aperture if the endpoints can be otherwise obscured, such as if the line extends beyond a certain eccentricity, particularly if the line’s contrast is tapered towards its endpoints, since the visual system has a lower acuity and higher contrast detection threshold for stimuli in the periphery (see Anstis, 2003). Similarly, such a line, if presented as a stationary reference for other moving elements, will provide no positional reference cues along the axis of its orientation. Since object-relative motion by definition requires reference points and non-object-relative motion by definition requires the absence of reference points, any motion orthogonal to that axis will be object-relative and (in the complete absence of all other visual references) any motion parallel to that axis will be non-object-relative motion. The differential processing model dictates that any unidirectional motion oblique to the line will be parsed by the visual system into a non-object-relative component parallel to the line and an object-relative component orthogonal to the line. Further, because of the visual system’s greater responsivity to object-relative than to non-object-relative motion, the velocity component parallel to the line (non-object-relative) will be perceptually reduced in comparison to that orthogonal to the line (object-relative). The direction of a stimulus such as a set of dots drifting obliquely to the line should therefore be shifted perceptually towards the orthogonal, i.e. the direction of the dots should be ‘repelled’ by the orientation of the line (Figure 3). This predicted shift in perceived direction of a single set of dots invoked by the presence of the static line we will refer to as the statically-induced direction illusion. The distribution-shift model, on the other hand, makes no such prediction since, by definition, it requires the presence of two directions of motion. The current experiment was designed to test for the occurrence of a statically-induced direction illusion and, if one was observed, to ascertain how the angular difference between the orientation of the inducing line and the test direction affects the magnitude of the illusion. This would enable us both to draw

comparisons with previously obtained angular functions of the conventional direction illusion and to determine the optimal stimulus parameters for use in later experiments.

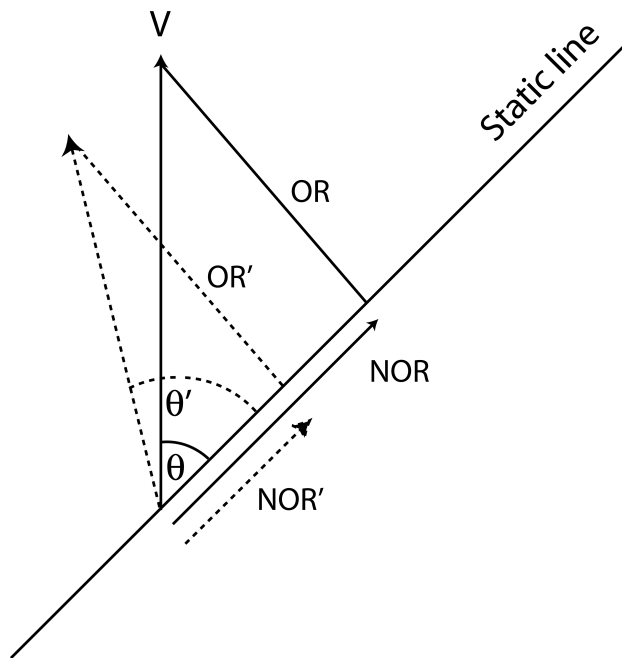


Figure 3. The dissociation of object-relative (OR) and non-object-relative (NOR) component velocities of a drifting stimulus due to the presence of a stationary line. The veridical velocity (V) is vertically upward, while its object-relative and non-object-relative component velocities are respectively orthogonal and parallel to the static line. We hypothesise that the non-object-relative component velocity will be perceptually underestimated (as NOR') with respect to the object-relative component, resulting in the angular separation of the drifting stimulus direction and the orientation of the line (θ) being perceptually exaggerated (θ').

2.1 Method

2.1.1 Apparatus All stimuli were generated and presented and all responses recorded with Psykinematix version 1.1.0 (build 1011) (KyberVision, Montreal, Canada, psykinematix.com). The software was run on a G5 Macintosh Dual 2 GHz Power PC running Mac OS X version 10.4.11. The SONY Trinitron Multiscan G520 monitor had a frame refresh rate of 75Hz and a pixel resolution of 1152x870. Participants viewed the screen binocularly from a distance of 57cm through a cylinder (diameter 30cm, length 57cm) that was lined internally with matte black felt, and a chin and headrest prevented head movement.

2.1.2 Stimuli A unidirectional white-on-grey RDK (test stimulus) comprising a coherently drifting set of 40 Gaussian dots was presented within an 8-deg virtual aperture with no visible boundary. All dots had a peak luminance of 104 cd/m^2 , with a standard deviation of 6 min arc and a drift speed of 0.5 deg/s. The background luminance was 65 cd/m^2 , giving a Michelson contrast of 23.1%. Dependent upon each observer's responses, the test stimulus drifted in a range of directions close to upward vertical (0°). The inducing stimulus was a static white line (length 27.78 deg, and width 0.12 deg) whose midpoint was located in the centre of the display. The luminance profile along the line's length followed a sin curve (0.018 cpd) with maximum contrast (23.1%) at the line's midpoint, decreasing to 0% contrast at each endpoint. The line was presented at one of eight orientations (3, 7.5, 15, 30, 45, 60, 75, and 90°) relative to the test direction (positive values indicate clockwise (CW) directions). A baseline condition incorporating an RDK but no inducing line was also presented.

2.1.3 Observers Twenty-two 2nd-year psychology students at Macquarie University completed the experiment. All were inexperienced observers and none were aware of the purpose of the study. All were emmetropic or had corrected-to-normal vision.

2.1.4 Procedure Each trial began with a brief tone and a 500 ms presentation of a uniform grey field with a small point in the centre of the screen. Test stimuli were then presented for 500 ms, during which time the central point was not present. Observers were instructed to remain fixated as near as possible to where the point had initially been presented. Being the centre of the display, this point coincided with the midpoint of the static line. Each successive trial began once a response was made. The seven test conditions were fully randomised within a single block of trials. The baseline condition was run in a separate block. This study used a standard staircase method (Wetherill & Levitt, 1965) to estimate each observer's point of subjective vertical. Observers indicated, using the left and right arrow keys, which side of upward vertical (0°) they

perceived the test stimulus to be moving. Observers completed two randomly interleaved 1-up-1-down staircases with respective starting values of $\pm 10^\circ$ from vertical, for each condition. Initial step size was 5° , reducing to 4, 3, 2, and a minimum of 1° on subsequent reversals. Each staircase terminated after 12 reversals, with the direction of the test stimulus on the final 6 reversals from each staircase being averaged for each observer to serve as an estimate of perceived vertical. Obtained means were adjusted by subtracting individual values of perceived vertical measured in the baseline condition.

2.2 Results and discussion

The results from Experiment 1 are reported in Figure 4. Directional shifts were small or absent when test/inducer separations were either very small ($\leq 15^\circ$) or very large (90°). However, intermediate separations yielded large CCW shifts in perceived direction. A set of one-sample two-tailed t-tests showed CCW shifts significantly different from zero for each of the 30, 45, 60, and 75° conditions ($t_{(19)} \geq 6.43$, $p < 0.0005$, $\eta^2 \geq 0.685$), and no significant shift for the 3, 7.5, 15, or 90° conditions ($t_{(19)} \leq 2.29$, $p \geq 0.034$) (p-values were Bonferroni-adjusted to control for overall error rate). Two of the observers produced anomalous data that indicated an obvious inability or reluctance to follow the instructions. Their data were therefore omitted from the analysis.

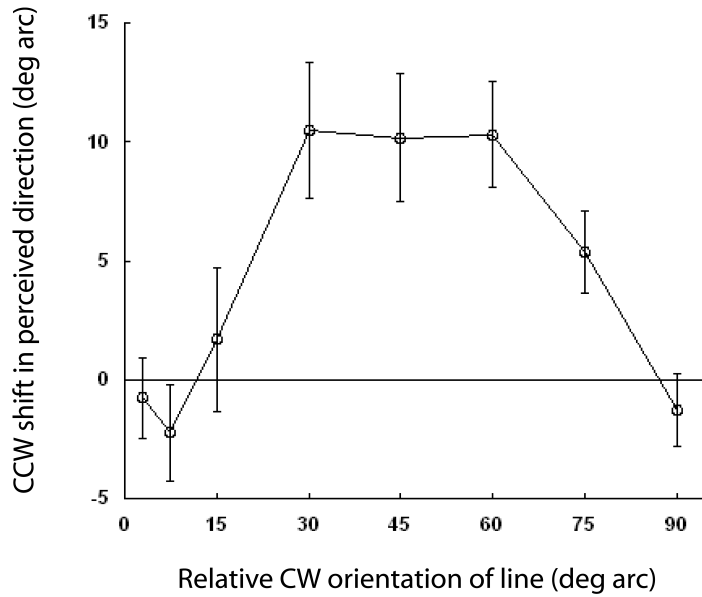


Figure 4. Graph showing the results of Experiment 1. Error bars represent 95% confidence intervals.

The primary aim of the current experiment was to test for the occurrence of a statically-induced direction illusion, which we found. Since mutual inhibition between direction-selective channels could only occur when two directions of motion are presented together, the illusions observed here cannot be accounted for by the distribution-shift model. On the other hand, the occurrence of the phenomenon is predicted by the differential processing model. The peak illusory effect was only $\sim 10^\circ$, while the peak effect obtained in most direction illusion studies is $\sim 20^\circ$ (Grunewald, 2004; Hiris & Blake, 1996; Marshak & Sekuler, 1979; Mather & Moulden, 1980; Rauber & Treue, 1998; Wiese & Wenderoth, 2007) (see also our results from Experiment 2). Discrepancies between the angular functions of the statically-induced direction illusion and those previously reported for the conventional direction illusion are not surprising, however, due to the differences between the stimuli used to invoke the respective illusions.

3 Experiment 2

Having demonstrated the existence of a statically-induced direction illusion, we wished to determine whether the magnitude of a conventional direction illusion could be increased and/or reduced by including differently orientated visual reference cues in the display. Here, we investigated the effects of the orientation of a static line on the perceived direction of one of the sets of dots in a bidirectional RDK.

According to the logic of the differential processing account, the introduction of a static line oriented parallel to the object-relative component velocity direction in a bidirectional RDK (parallel to BC in Figure 2), will provide a reference cue for motion in the non-object-relative component direction (AD in Figure 2), transforming what was initially non-object-relative motion into object-relative motion. What was initially the object-relative component velocity should be unaffected since the line does not introduce any further reference for motion along its axis. The line should therefore diminish the size of the direction illusion. Conversely, a line parallel to the non-object-relative component velocity should not affect the direction illusion magnitude, since a line with such an orientation would provide no reference along the axis of the non-object-relative component velocity. It would only provide an additional reference along the axis of the object-relative component velocity where reference cues are already available. However, there is a possibility that the additional reference will slightly increase the object-relative component velocity, thereby marginally increasing the size of the direction illusion.

The distribution-shift model, however, contends that the mutual inhibition that arises in a bidirectional RDK is driven by the veridical velocities of the two sets of dots invoking responses in direction-selective channels. As these units show no response to stationary features, this model cannot predict that the presence of a static line of any orientation should have an influence on the magnitude of the direction illusion.

The current experiment was designed to determine whether or not the magnitude of the direction illusion observed in a bidirectional RDK would be reduced by the presence of a static line oriented orthogonally to the non-object-relative component velocity, and either increased or unaffected with the line oriented parallel to the non-object-relative component velocity.

3.1 Method

The apparatus was identical to that in Experiment 1, but several changes were made to the stimulus configuration. Here we used bidirectional RDKs with one set of dots considered the test stimulus and the other the direction illusion inducer, which drifted at 30° relative to the test direction. The 30° direction separation was chosen on the basis that the same separation yielded the largest statically-induced direction illusion in Experiment 1. The experiment included three conditions, one of which consisted of the bidirectional RDK alone (Figure 5A), and two of which also incorporated the static white line, which was oriented at either -75° or 15° relative to the test direction (see Figure 5B and C). The two orientations were specifically selected to match the direction of the object-relative and non-object-relative component velocities, respectively. The three test conditions were fully randomised within a single block of trials. Obtained means were adjusted by subtracting individual values of perceived vertical measured in the baseline condition in Experiment 1.

3.1.1 Observers Twenty-one of the 22 observers who participated in Experiment 1 also participated in Experiment 2.

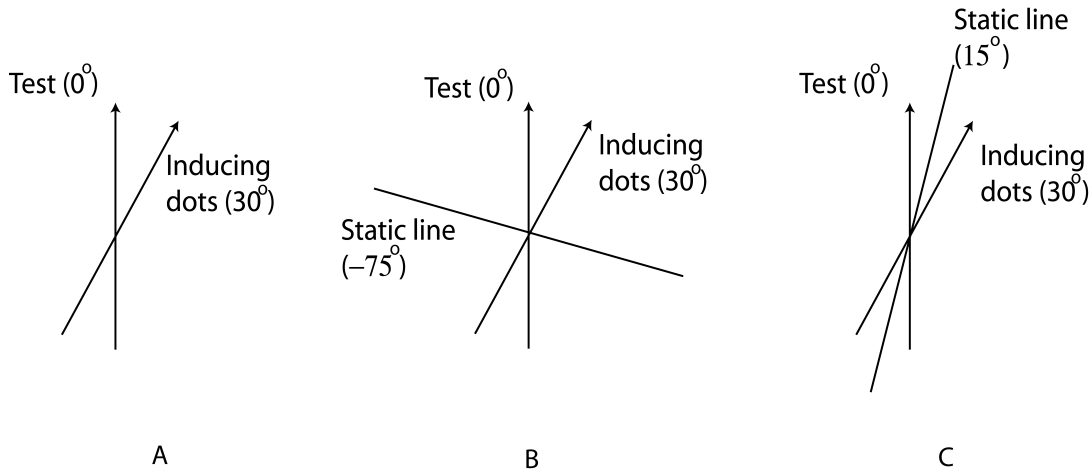


Figure 5. Schematic diagram of the three test conditions in Experiment 2: (A) Bidirectional RDK with test direction 0° and inducing dots direction 30° relative to test direction. (B) Bidirectional RDK with a static line oriented at -75° relative to the test direction, i.e. aligned with the object-relative component velocities. (C) Bidirectional RDK with a static line oriented at 15° relative to the test direction, i.e. aligned with the non-object-relative component velocity.

3.2 Results and discussion

Data from five of the observers, including those omitted in Experiment 1, were omitted from the current analysis, the reason being that three observers produced results in the direction illusion condition indicating a CW shift in perceived direction, opposite to the expected shift². Results from Experiment 2 are reported in Figure 6. For the no-line (direction illusion) condition we obtained a mean CCW directional shift of 22.0°, which is similar in size to previous measurements of the direction illusion with the same directional separation of 30° (Braddick, Wishart, & Curran, 2002; Grunewald, 2004; Rauber & Treue, 1999; Wiese & Wenderoth, 2007). With a line oriented at 75° CCW of the test direction we obtained a mean CCW directional shift of 3.7°, and with a line oriented at 15° CW of the test direction we obtained a mean CCW directional shift of 17.4°. A set of one-sample two-tailed t-tests showed the direction illusion in the no-line condition ($t_{(15)} = 5.511$, $p < 0.0005$, $\eta^2 = 0.669$), and in the 15° CW condition ($t_{(15)} =$

² The aim of our study was to compare the capacity of two models to predict characteristics of the direction illusion as it is generally observed. As no previous study has reported an attraction effect when the inducer and test directions are separated by 30°, we considered it prudent to omit these data. However, when these results are included, there is no appreciable change in the pattern of results obtained, or in the statistical significance of the findings.

5.203, $p < 0.0005$, $\eta^2 = 0.643$) to be significantly different from zero. However, the small shift in the 75° CCW condition was not significantly different from zero ($t_{(15)} = 1.861$, $p = 0.082$), signifying that the presence of the line in this condition was effective in eliminating the direction illusion. Two-tailed t-tests showed a significant difference between the no-line and 75° CCW condition ($t_{(15)} = 6.806$, $p < 0.0005$) but no significant difference between the no-line and 15° CW condition ($t_{(15)} = 1.432$, $p = 0.173$).

While the results of the no-line and 15° CW conditions are consistent with a distribution shift, the model cannot account for the results of the 75° CCW condition. On the other hand, the results of all three conditions are readily interpretable if we attribute the direction illusion to differential processing. As predicted by this model, the direction illusion was significantly reduced in the 75° CCW condition, possibly because the non-object-relative component velocity is no longer underestimated when the line is added, since the line effectively transforms this component into an object-relative motion. The direction illusion was unchanged by the presence of the 15° CW line. We can infer from this finding that the object-relative component velocity was unchanged by the additional reference cue.

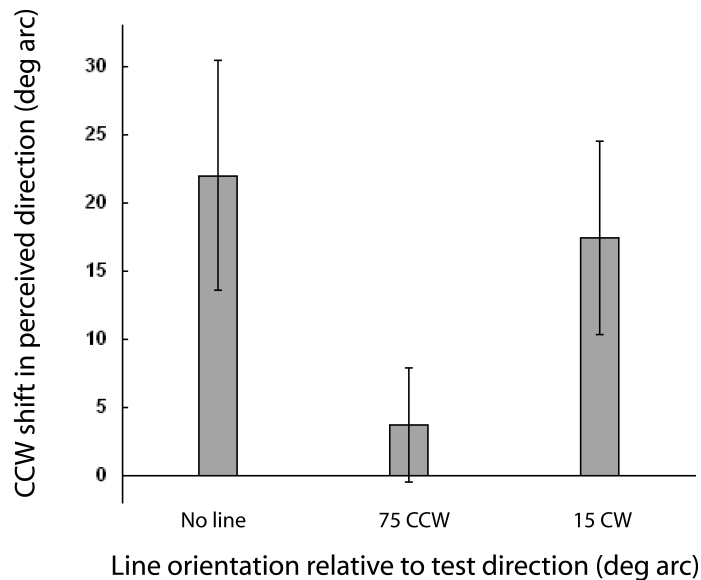


Figure 6. Graph showing the results of Experiment 2. Error bars represent 95% confidence intervals.

4 Experiment 3

As described earlier, the distribution-shift model attributes the direction illusion to mutual inhibition between direction-selective cell populations. The previous two experiments have respectively demonstrated the inability of this model to account for the capacity of a static line to invoke a direction illusion (Experiment 1) and to eliminate the direction illusion in a bidirectional RDK (Experiment 2). One way in which we might attempt to reconcile these findings with the distribution-shift model is by considering the possible involvement of mutual inhibition not between direction-selective channels but between orientation-selective channels. We will refer to this proposed mechanism as an orientation distribution shift. Geisler (1999) proposed that moving stimuli produce neural ‘motion streaks’ within the visual system. He suggested that motion streaks should result from the temporal integration of motion signals activating orientation-selective neurons that are tuned to orientations parallel to the direction of motion. If

motion stimuli could activate orientation-selective channels, then we should expect to observe perceptual interactions between direction and orientation domains. Geisler provided evidence for the occurrence of motion streaks by measuring the luminance detection threshold of a moving Gaussian dot as a function of its size and speed when it was presented with a grating mask at various orientations relative to the dot direction. When the dot moved above a certain critical speed of approximately 1 ‘dot width’ per 100 ms (a dot width was defined as 4 times the dot’s Gaussian standard deviation) a parallel mask was significantly more effective in elevating thresholds than was an orthogonal mask, with intermediate mask orientations producing intermediate threshold elevations. Geisler found further evidence for the occurrence of motion streaks in an orientation adaptation experiment. After adaptation to a grating oriented 10° from vertical, observers judged the direction of a vertically moving 12-min dot. The dot had a speed of either 2.5 or 10 deg/s, which according to Geisler’s estimations should produce, respectively, weak and strong motion streaks. While the faster dots showed a shift of $\sim 2.2^\circ$ in perceived direction, the slower dots were perceptually shifted by only $\sim 0.4^\circ$. The former result is comparable in size to the tilt aftereffect, which is a repulsive shift in the orientation of a line or grating due to previous adaptation to a differently oriented line or grating (e.g. Gibson & Radner, 1937). Athorp and Alais (2009) produced further evidence of motion streaks activating orientation-selective channels by showing a similar shift in the perceived orientation of a central grating due to simultaneously presented RDK motion surrounding the grating. They obtained an angular function for the effect, which we refer to hereafter as a motion-induced tilt illusion. The results were very similar to those produced in studies of the tilt illusion, which was defined in Section 1.1 (O’Toole & Wenderoth, 1977; Over, Broerse, & Crassini, 1972). Further evidence for direction/orientation interactions comes from studies using static configurations of paired dots that, when flashed in succession, invoke motion percepts whose direction is determined by the

orientation of the dot pairs (e.g. Burr & Ross, 2002; Johnson & Wenderoth, 2011; Ross, Badcock, & Hayes, 2000).

The statically-induced direction illusions observed in Experiment 1 are an order of magnitude larger than the direction and orientation shifts associated with the occurrence of motion streaks. Also, in Experiments 1 and 2 we selected values for dot width and speed that would not meet the criteria for producing motion streaks. Remembering that the critical speed is calculated as 1 “dot width” per 100 ms and that a dot width is defined as 4 times the dot's Gaussian standard deviation, for a Gaussian dot with a standard deviation of 6 min arc, the “dot width” is 24 min arc. The critical speed was thus 24 min arc per 100 ms, or 4 deg/s. We are therefore confident that the observed effects were not produced, at least not entirely, by this mechanism. However, we wanted to address directly the possible involvement of motion streaks in the production of the statically-induced direction illusion. To this end, we compared the size of the illusion when invoked with RDKs with speeds above and below the critical speed for producing motion streaks. If the illusion is due, at least in part, to mutual inhibition between orientation-selective channels responding to both the static line and motion streaks produced by the drifting dots, i.e. to an orientation distribution shift, we would expect to obtain a larger illusion with the faster dots than with the slower dots. The differential processing model, on the other hand, makes no specific predictions regarding the effects of speed. A further objective was to determine whether the RDK invokes a motion-induced tilt illusion in the static line. If the statically-induced direction illusion arises from an orientation distribution shift due to the presence of motion streaks, we should expect to observe a motion-induced tilt illusion and, as with the statically-induced direction illusion, it should be larger with faster dots than with slower dots. If the statically-induced direction illusion arises entirely from differential processing, however, no motion-induced tilt illusion is expected.

4.1 Methods

4.1.1 Apparatus and stimuli The apparatus was the same as that used in Experiments 1 and 2. The stimuli differed from those in Experiments 1 and 2 as follows: Here the Gaussian dots had a standard deviation of 3 min arc. Drift speed was either slow (0.5 deg/s) or fast (8 deg/s), respectively below and above the critical speed of 2 deg/s required to produce motion streaks. In the statically-induced direction illusion conditions, the static line was always oriented at 30° relative to the direction of the RDK, and in the motion-induced tilt-illusion conditions, the direction of the RDK was always 30° relative to the orientation of the line.

4.1.2 Observers Five observers, 3 male and 2 female, took part in the experiment. We were confident in using a small group of participants, because the task was relatively simple, and because a pilot study produced robust outcomes. Four of the observers were staff or students at Macquarie University and had previous experience with similar experimental tasks. One participant was the author, and one other was aware of the purpose of the experiment. One observer had had no previous experience. All were emmetropic or had corrected-to-normal vision.

4.1.3 Procedure We used four test conditions, labeled SDI slow (statically-induced direction illusion with slow-moving dots), SDI fast (statically-induced direction illusion with fast-moving dots), MTI slow (motion-induced tilt illusion with slow-moving dots), and MTI fast (motion-induced tilt illusion with fast-moving dots). We also ran three baseline conditions: the two statically-induced direction illusion conditions with the static line absent and a motion-induced tilt illusion condition with the RDK absent. In the direction illusion conditions observers judged the direction of the RDK, and in the tilt illusion conditions they judged the line's orientation. The seven conditions were run in separate blocks, which were presented in random order. The procedure was similar to that in Experiments 1 and 2. In each of the experimental

conditions, observers completed two randomly interleaved staircases with starting values of $\pm 20^\circ$ from vertical. Initial step size was 32° , and was halved for each subsequent reversal, with a minimum step size of 1° . Obtained values for each condition were averaged for each observer and adjusted by subtracting individual values obtained from the corresponding baseline conditions.

4.2 Results and discussion

Results from Experiment 3 are reported in Figure 7. For the SDI slow condition we obtained a mean CCW directional shift of 13.47° , which is comparable in size to that observed in Experiment 1, and in the SDI fast condition we obtained a mean CCW shift of 2.56° . One-sample two-tailed t-tests showed a significant difference from zero for each of the SDI slow ($t_{(4)} = 7.763$, $p = 0.001$, $\eta^2 = 0.938$), and SDI fast ($t_{(4)} = 7.034$, $p = 0.002$, $\eta^2 = 0.925$) conditions. A paired t-test showed there was a significant difference in the directional shift between the SDI slow and SDI fast conditions ($t_{(4)} = 6.463$, $p = 0.003$, $\eta^2 = 0.913$). For the MTI slow condition we obtained a mean directional CW shift of 0.03° , and in the MTI fast condition we obtained a mean CW shift of 0.06° . One-sample two-tailed t-tests showed no significant difference from zero for either the MTI slow ($t_{(4)} = 0.059$, $p = 0.956$) or MTI fast ($t_{(4)} = 0.098$, $p = 0.926$) conditions.

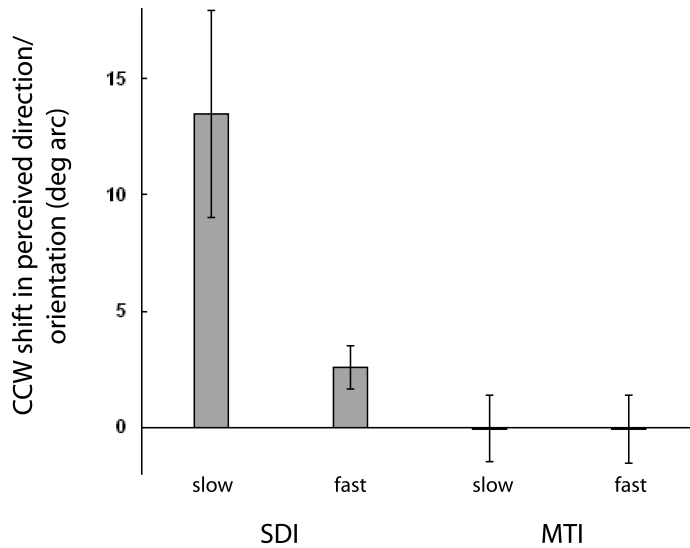


Figure 7. Graph showing the results of Experiment 3. Error bars represent 95% confidence intervals.

Our failure to observe a motion-induced tilt illusion in either the MTI slow or MTI fast condition indicates either that no motion streaks are produced by our drifting dot stimuli, or that motion streaks are produced but fail to affect the perceived orientation of the line. If the former is the case, then we can immediately discount the involvement of an orientation distribution shift in producing the statically-induced direction illusion. If the latter is the case, there remains the possibility that the statically-induced direction illusion is produced by an orientation distribution shift but that the shift is asymmetrical, affecting the perceived orientation of the motion streaks, and therefore the perceived direction of the dots, without affecting the perceived orientation of the line. The SDI slow condition yielded a significant shift in perceived direction, indicating that the illusion is not due to the presence of motion streaks, as stimuli at this speed are incapable of forming any such features. Moreover, the shift was an order of magnitude larger than previously reported direction and orientation shifts associated with the interaction of motion streaks and static oriented stimuli (e.g. Apthorp & Alais, 2009), indicating again that the effects shown in the

current study cannot be explained in this way. Conversely, the stimuli in Experiment 3 that were predicted to produce strong motion streaks (SDI fast condition) in fact produced a very much reduced direction illusion. That the SDI slow condition produced a much larger shift than the SDI fast condition clearly contradicts the predictions of the orientation distribution-shift hypothesis and indicates that the statically-induced direction illusion does not arise from the mutual inhibition of orientation-selective cell populations resulting from the occurrence of motion streaks. In contrast, none of the conditions produced data that conflict with the differential processing model. The model makes no predictions of any orientation shift in either of the motion-induced tilt illusion conditions. Further, the SDI slow and SDI fast data are not inconsistent with the differential processing model. Although differential processing explicitly predicts a statically-induced direction illusion in both slow and fast conditions, it makes no specific quantitative prediction regarding the effect of dot speed and, in particular, the relative size of the effects in slow and fast conditions. Further research into the effects of speed on both object-relative and non-object-relative velocities is required before the model can be extended to make any such predictions. However, the current findings echo those previously reported in the context of the direction illusion. Our data show an increase in statically-induced direction illusion magnitude as the RDK speed is reduced from 8 deg/s to 0.5 deg/s. Rauber and Treue (1999) and Braddick, Wishart, and Curran (2002) also found that reducing the speed of both sets of dots in a bidirectional RDK increased the size of the conventional direction illusion considerably. The inverse relationship reported here of stimulus speed to the size of the shift in perceived direction is thus consistent with the proposal that the statically-induced direction illusion and the conventional direction illusion share a common mechanism.

5 General Discussion

Dakin and Mareschal (2000) argued that mutual inhibition between direction-selective channels does not explain certain aspects of the direction illusion and proposed instead that the phenomenon arises as a result of the differential processing of object-relative and non-object-relative motion components. Without evidence solid enough to refute the distribution-shift model (see Section 1.2), however, subsequent studies have continued to attribute the direction illusion to mutual inhibition between direction-selective channels (e.g. Braddick, et al., 2002; Chen, Matthews, & Qian, 2001; Curran, Clifford, & Benton, 2006; Curran, Clifford, & Benton, 2009). The primary aim of the current paper was to evaluate and compare the tenability of the distribution-shift and differential processing models of direction perception, particularly as they apply to the direction illusion. In Experiment 1, we observed a statically-induced direction illusion, an effect predicted by the differential processing model but not by the distribution-shift model. In Experiment 2, we found that introducing a static line parallel to the object-relative component direction of a direction illusion-invoking bidirectional RDK eliminated the illusion, while a line parallel to the non-object-relative component had no effect on the illusion. Again, the results are consistent with differential processing but not with mutual inhibition between direction-selective channels. In Experiment 3, we investigated the possibility that the results of Experiments 1 and 2 may be accounted for by the distribution-shift model applied to the orientation domain, hypothesising that the statically-induced direction illusion might arise from mutual inhibition between orientation-selective channels due to the existence of motion streaks. We measured the illusion with slow and fast moving dots and found the former to produce a larger effect. We also tested for the occurrence of a motion-induced tilt illusion due to slow and fast dot motion but found no effect. The results conflicted with the orientation distribution-shift hypothesis but were consistent with the differential processing model.

5.1 A third model – the clustering algorithm

One group of researchers (Mahani, Carlsson, & Wessel, 2005) has argued against the distribution-shift model, suggesting instead that the direction illusion occurs as a direct consequence of solving the motion transparency problem. They claim that implementation of a particular clustering algorithm, an iterative statistical process that is required to estimate the direction and group identity of the individual dots, necessarily leads to an exaggeration of the directional difference between the two dot sets. In other words, the direction illusion is a statistically inevitable by-product of the process of integration and segmentation of the independent elements in transparent motion. The results of Experiments 1 and 3, however, clearly demonstrate that directional shifts occur without any need for group identification since there was only one group present. In addition, the direction illusion was eliminated in Experiment 2 by the orientation of a static line, a result on which the clustering algorithm is silent. As such, the current results cannot be accounted for by the model of Mahani et al. (2005).

5.2 Conclusion

We have shown that a static line can invoke shifts in the perceived direction of a moving stimulus and can eliminate the directional shift observed in a conventional direction illusion-inducing configuration. We have further shown that the direction shifts invoked by the static line cannot be explained by the existence of motion streaks. These findings cannot be attributed to a distribution shift resulting from mutual inhibition between either direction-selective or orientation-selective channels, and they pose serious questions about the distribution-shift model's adequacy in accounting for perceived direction in general. Conversely, the results reported here are consistent with the occurrence of differential processing of object-relative and non-object-relative component velocities by the visual system. Since moving objects usually have

veridical velocities that comprise both types of motion, and since the latter type has been found to be underestimated with respect to the former, the differential processing model dictates that the perceived direction of such objects will be shifted from the veridical. We will be assessing the tenability of this model further in a future study on the effects of such processes on perceived stimulus velocity, i.e. direction and speed (Farrell-Whelan, Wenderoth and Brooks, in preparation).

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4 A quantitative differential processing model of perceived velocity

In the previous paper, we showed that the neural mechanism commonly thought to underlie the DI, i.e. a response distribution shift in a population of cells tuned to the veridical directions of the stimulus motion, is unlikely to be responsible for the occurrence of the phenomenon. We showed that a static line induces a shift in the perceived direction of an RDK stimulus moving obliquely to the line's orientation, which we have termed the statically induced direction illusion (SDI). The results are in agreement with the involvement of differential processing since the occurrence of the SDI shows that the velocity component parallel to the static line is underestimated with respect to the component orthogonal to the line. However, the mere occurrence of the SDI (i.e. a shift in perceived direction) tells us nothing quantitative about the perceived velocity, nor of the perceptual NOR and OR component speeds, only that the NOR component speed is underestimated with respect to the OR component speed. A more formally defined model of differential processing will need to impose restrictions on the possible quantitative combinations of component speeds. One of these restrictions is that the perceived velocity must decrease as the angle between the test direction and line orientation decreases. Further, the model contends that the perceptual NOR component speed is underestimated as a constant proportion of the perceptual OR component speed. A stringent test of the model therefore requires that measurements be made of shifts both in perceived direction and perceived speed. This was the objective of the following study.

4.1 Manuscript 3

Farrell-Whelan, M., Wenderoth, P., & Brooks, K. R. Differential processing: Towards a unified model of direction and speed perception. Submitted for publication.

Differential processing: Towards a unified model of direction and speed perception

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Abstract. Spatial context influences the perceived velocity of moving objects. A static line, for example, can induce a shift in the perceived direction of a random-dot stimulus moving obliquely to the line's orientation, termed the statically-induced direction illusion (SDI). We propose that the illusion is due to the differential processing of object-relative and non-object-relative component velocities, with the latter being perceptually underestimated with respect to the former by a constant ratio. Although previous proposals have not allowed quantitative accounts, we present a unified formal model of perceived velocity (both direction and speed) with the magnitude of this ratio as the only free parameter. The model was successful in accounting for the angular repulsion of motion direction by an oriented line (Experiment 1), and in predicting a reduction in perceived velocity when the line's orientation was similar to the motion direction (Experiment 2). Fitting produced a similar best-fit value of the ratio of underestimation of non-object-relative motion (compared to object-relative motion), confirming that this model is capable of simultaneously accounting for misperceptions of velocity whether they are measured in terms of direction or speed.

Keywords: differential processing; static direction illusion; direction illusion; relative motion; induced motion

1 Introduction

Whenever we view a moving object our perception of its velocity, i.e. its speed and direction, is determined by the object's veridical velocity, being its velocity with respect to the observer, its intrinsic properties (size, shape, luminance, etc.), and by the spatial and temporal context in which it is viewed. Findings from a number of psychophysical studies (e.g. Blakemore & Snowden, 2000; Brown, 1931; Gogel & McNulty, 1983; Nguyen-Tri & Faubert, 2007; Norman, Norman, Todd, & Lindsey, 1996) suggest that an object is perceived as having a comparatively higher speed when viewed in motion relative to other objects, termed object-relative (OR) motion, than when viewed in motion in the absence of such reference cues, termed non-object-relative (NOR) motion (see Farrell-Whelan, Wenderoth, & Brooks, 2012 for a brief review of these studies). As a naturalistic example of how an object's spatial context can influence its perceived velocity, picture a bird flying high overhead as you look up at the clouds on a windless day. Against the backdrop of clouds, the bird's motion is OR. A bird flying at the same velocity on a cloudless day, and therefore in NOR motion, should appear to be travelling more slowly.

Psychophysical research has also uncovered a considerable number of other differences in the way we perceive OR and NOR motion. Direction discrimination thresholds (Beardsley & Vaina, 2008; Snowden, 1992), displacement thresholds (Lappin, Donnelly, & Kojima, 2001; Legge & Campbell, 1981; Murakami, 2004; Palmer, 1986; Sokolov & Pavlova, 2006; Whitaker & MacVeigh, 1990) and reaction times (Smeets & Brenner, 1994) are lower for OR than for NOR motion, and changes in contrast (Grossman & Blake, 1999; Shioiri, Ito, Sakurai, & Yaguchi, 2002), spatial frequency (Shioiri, et al., 2002) and stimulus size (Mestre, Masson, & Stone, 2001; Murakami & Shimojo, 1996; Nawrot & Sekuler, 1990) affect OR and NOR motion perception differently. Other differences occur during binocular rivalry – if one eye is presented

with an OR motion stimulus and the other with NOR motion, the former becomes the dominant percept (e.g. Baker & Graf, 2008; Paffen, te Pas, Kanai, van der Smagt, & Verstraten, 2004). Further, the strength of motion aftereffects is greater after OR than after NOR motion adaptation (e.g. Day & Strelow, 1971), and OR motion channels can be selectively adapted (Shioiri, Ono, & Sato, 2002). These findings show that OR and NOR motion are encoded differently by the visual system, implicating the involvement of separate neural processes.

Often the visual scene includes motion trajectories of many objects and therefore many combinations of OR and NOR motion. In visual motion studies, one frequently used stimulus configuration comprising both OR and NOR component velocities is the bidirectional random dot kinematogram (RDK) – a display consisting of two superimposed sets of random dots, with each set translating in a different direction. This generates a percept of two sheets of dots sliding across one another, which is referred to as motion transparency. Figure 1 shows how this configuration creates orthogonal OR and NOR component velocities. The veridical velocities of the two sets of dots are represented by the vectors \mathbf{z}_1 and \mathbf{z}_2 . The NOR component velocity, i.e. the velocity component that is common to both sets, is represented by the vector \mathbf{x} , and the OR component velocities unique to each set, are represented by the vectors \mathbf{y}_1 and \mathbf{y}_2 . Johansson (1950) was among the first to describe visual motion trajectories as compositions of NOR and OR component velocities, and he, along with many researchers since (e.g. Cutting & Proffitt, 1982; Gogel, 1979; Grossberg, Léveillé, & Versace, 2011; Takemura & Murakami, 2010), has contended that the visual system must somehow dissociate the two velocity types. If such a dissociation does occur, and if NOR component velocities are underestimated in comparison to OR component velocities, we would predict that any motion comprising both a NOR and an OR component will be shifted perceptually from its veridical trajectory. This is in fact what is observed in a bidirectional RDK. The phenomenon, which is often referred to as the direction

illusion, manifests as an overestimation of the angle between the two directions of RDK motion (Marshak & Sekuler, 1979; Mather & Moulden, 1980). Figure 1 shows that if the magnitude of the NOR component x is perceptually underestimated ($x' < x$) but the perceptual OR component speeds are not ($y_1' = y_1$ and $y_2' = y_2$), the result is a perceptual exaggeration of $\theta_1 + \theta_2$ as $(\theta_1 + \theta_2) + (\alpha_1 + \alpha_2)$.

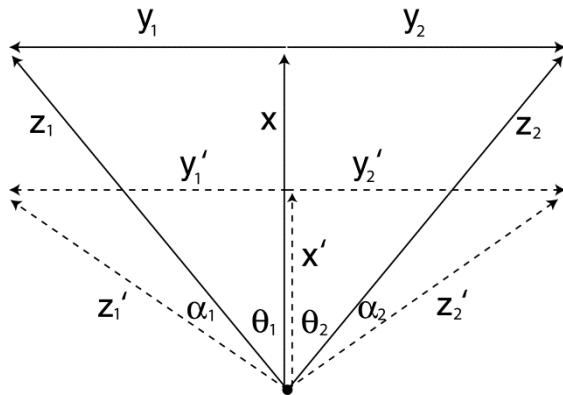


Figure 1. Vector diagram of the differential processing account of the direction illusion. Vectors z_1 and z_2 represent the veridical velocities in the bidirectional RDK. In comparison to the magnitude of OR component velocities y_1' and y_2' , the magnitude of the NOR component x is perceptually underestimated, as shown by the vector x' . This results in a perceptual exaggeration of the angle $\theta_1 + \theta_2$ as $(\theta_1 + \theta_2) + (\alpha_1 + \alpha_2)$ (adapted from Dakin & Mareschal, 2000).

In a recent literature review, Nishida (2011) reported that the direction illusion ‘is considered to reflect repulsive interactions between two directions (Wilson & Kim, 1994) or functional computation of target motion relative to the background motion (Dakin & Mareschal, 2000).’ These alternative accounts of the direction illusion we refer to respectively as the distribution-shift model and the differential processing model. The distribution-shift model contends that the direction illusion arises from an inhibitory interaction between cell populations that respond to the two veridical directions in a bidirectional RDK (e.g. Mather, 1980; Mather & Moulden, 1980). Each population response can be represented by a Gaussian-like distribution,

which becomes skewed by neuronal inhibition when the two directions are presented simultaneously (see Snowden, Treue, Erickson, & Andersen, 1991). As a result, the peaks of the two response distributions shift apart, producing a perceptual overestimation of the directional difference between the two directions. Since it was first reported, the direction illusion has been attributed to such a distribution shift (Grunewald, 2004; Hiris & Blake, 1996; Kim & Wilson, 1996; Kim & Wilson, 1997; Marshak & Sekuler, 1979; Mather & Moulden, 1980; Patterson & Becker, 1996; Wilson & Kim, 1994). The differential processing model (Dakin & Mareschal, 2000; Farrell-Whelan, et al., 2012), on the other hand, adopts Johansson's assertion that such shifts in perceived direction result from the dissociation of NOR and OR velocity components and that the former is comparatively underestimated, as described above. This model implicates an entirely different neural mechanism from the distribution shift account since it requires the extraction of component velocities, which may differ considerably from the veridical velocity.

In a previous study (Farrell-Whelan, et al., 2012), we introduced a stimulus consisting of orthogonal NOR and OR components: a field of coherently moving random dots referenced by a straight, static line that extends into the periphery at either end. When a moving line is viewed through a circular aperture, because its endpoints are obscured there are no cues to any motion of the line parallel to its orientation. It will therefore appear to move in a direction orthogonal to its orientation. This is the well-known 'aperture problem' (Wallach, 1935). Similarly, since the endpoints of a static line of sufficient length will also be obscured, in this case by their eccentricity from foveal viewing, they will provide no positional cues for motion parallel to the line's axis. Therefore, any component of motion parallel to that axis will be, by definition, NOR. However, since the line does provide a positional cue for motion orthogonal to its axis, motion components in this direction will be OR. The differential processing model dictates that motion oblique to the line will be parsed into its NOR and OR components, respectively parallel and

orthogonal to the line, and that the NOR component velocity will be perceptually underestimated in comparison to the OR component velocity. As a result, the perceived direction of a stimulus moving obliquely to the line should be shifted away from the line's orientation and towards the orthogonal. We investigated the effects of a static line on the perceived direction of a single set of random dots, observing shifts in perceived direction towards the orthogonal often of more than 10° . We have termed this phenomenon the statically-induced direction illusion (SDI). While these findings are well predicted by the differential processing model, the distribution-shift model, which requires the presence of two motion directions, cannot account for the occurrence of this illusion.

In a separate experiment, we incorporated a static line into a conventional direction illusion-generating bidirectional RDK. We found that when the line's orientation was orthogonal to the NOR component velocity, i.e. orthogonal to the vector \mathbf{x} in Figure 1, the direction illusion was eliminated. Again, the distribution-shift model cannot account for this effect since it makes no prediction regarding the line's influence. However, the differential processing account does predict this result since the line provides a reference cue, thereby transforming the NOR component into OR motion, which is consequently perceived as having a higher velocity.

We have previously reported the occurrence of the SDI, which is compatible, in qualitative terms, with the involvement of differential processing in the perception of motion direction. However, in doing so we recorded only directional shifts and did not determine what shifts in perceived speed may also have occurred. The differential processing model attributes the shift in perceived direction to the comparative underestimation of the NOR component velocity. That is, given veridically equivalent component speeds, the NOR component will have a lower perceptual speed. To illustrate, Figure 2 shows the upward veridical velocity (\mathbf{z}) of a stimulus in

the presence of a static line oriented at θ compared to this vector. Its NOR and OR component velocities are labelled \mathbf{x} and \mathbf{y} , respectively. The perceived velocity \mathbf{z}' has a perceived direction shifted α counter-clockwise (CCW) from vertical. The perceptual NOR and OR components of \mathbf{z}' are labelled \mathbf{x}' and \mathbf{y}' , respectively. The differential processing proposal (Farrell-Whelan, et al., 2012) can account for the occurrence of the SDI in qualitative terms because it dictates that x' is underestimated in comparison to y' . Although the SDI is consistent with the involvement of differential processing, the previous descriptions of this process lacked the ability to make quantitative predictions. In addition, although the differential processing proposal has implications for perceived speed, no attempt has yet been made to investigate these. In the current study, we present a model of perceived velocity that is more specific, allowing quantitative predictions regarding both perceived direction and perceived speed.

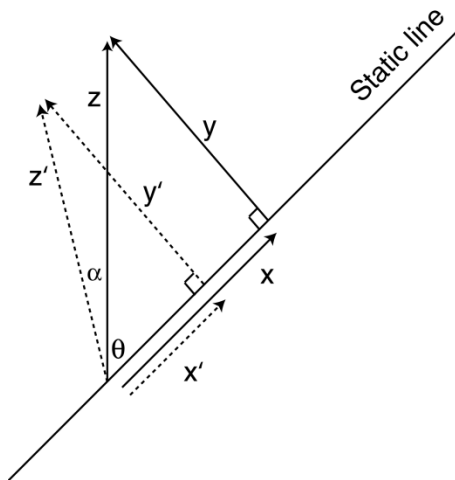


Figure 2. Vector diagram illustrating how differential processing may account for shifts in the perceived direction of a moving stimulus due to the presence of a static line. The veridical velocity (\mathbf{z}), which is directed vertically upward, is broken down into NOR (\mathbf{x}) and OR (\mathbf{y}) component velocities, which are respectively parallel and orthogonal to the static line. The differential processing model dictates that the perceptual speed of \mathbf{x} , labelled \mathbf{x}' , will be underestimated in comparison to the perceptual speed of \mathbf{y} , labelled \mathbf{y}' , resulting in the direction of motion relative to the orientation of the line (θ) being perceptually exaggerated (by α°).

We begin with the assumption that the perceptual component speeds are proportional to their respective veridical speeds across a broad range of stimulus velocities (including those used

in this study, and other typical psychophysical investigations). This assumption can be represented by the expressions $x' = c_x \cdot x$ and $y' = c_y \cdot y$, where c_x and c_y are constants. The proposal that the speed of NOR motion is perceptually underestimated with respect to OR motion can be formalised as $c_x < c_y$. Our previous, more broadly defined proposal that x is underestimated compared to y (which could be represented formally as $x'/x < y'/y$) is now more specifically defined as $x'/x = (c_x/c_y) y'/y$, where $c_x/c_y < 1$. Because both c_x and c_y are constants, c_x/c_y is also a constant. Lending validity to this assumption, De Bruyn and Orban (1999), matching perceived NOR (unidirectional RDK) speeds with perceived OR (180° bidirectional RDK) speeds, found that the former was perceived as a constant proportion (~0.667) of the latter across the entire range of speeds tested.

The simple proposal that $x'/x = (c_x/c_y)(y'/y)$ allows us to generate quantitative predictions of both direction and speed. Considering perceived direction α , it can be shown that $\alpha = \tan^{-1}(\tan\theta/(c_x/c_y)) - \theta$. Since the model has only one free parameter (c_x/c_y), we can test the goodness of fit of the model by comparing its predictions of α across a range of values of θ against predictions from the null hypothesis, that $x'/x = y'/y$ (i.e. that $c_x/c_y = 1$). We can also thereby obtain the best-fitting value of this parameter. In Experiment 1, which effectively constitutes a replication of Farrell-Whelan et al.'s (2012) Experiment 1, we measured α across a broad range of values of θ . We did this both to test the quantitative predictions made by our formal model, and to assess the claim that the best-fitting value of c_x/c_y is indeed smaller than 1.

In terms of perceived speed, the previous proposal that the magnitude of NOR motion (y) is underestimated relative to OR motion (x), allows us to make qualitative predictions about the pattern of results that we should expect. In general, perceived speed should be affected only minimally for conditions in which the veridical component of OR motion is large (compared to the NOR component), while those with a more substantial NOR component should appear

reduced in speed. However, the model as presented in the current paper allows more specific quantitative predictions. The differential processing model specifies that $x' = c_x \cdot x$ and that $y' = c_y \cdot y$ and, since it is true that $x = z \cdot \cos\theta$ and $y = z \cdot \sin\theta$, our model also dictates that $x' = c_x \cdot z \cdot \cos\theta$ and that $y' = c_y \cdot z \cdot \sin\theta$. Based on its predictions of component speeds across values of θ , the model necessarily also makes predictions about the relative perceived velocity across these values. Since $z'^2 = x'^2 + y'^2$, it can be shown that the relative perceived speed is given by $z'/c_y = z \sqrt{((c_x/c_y)^2 \cos^2\theta + \sin^2\theta)}$. In Experiment 2, these predictions were tested, again with the intention of assessing the ability of the model to account for speed perception, to check that the best-fitting value of c_x/c_y is indeed smaller than 1, and to verify that this free parameter value derived from Experiment 1 (direction) corresponds to that derived from Experiment 2 (speed). Note that it is not possible to determine an absolute speed of z' since speed judgments can only be made on a comparative basis. The value z'/c_y is a measure of the relative perceived speed that corresponds to the perceptual measurements taken in Experiment 2.

2 Experiment 1 – Direction

The aim of the first experiment was to obtain measurements of statically-induced shifts in the perceived direction of the test stimulus (α) across several angular separations of test direction and inducer orientation (θ) (Figure 3). From these values, we attempt to fit our model to the data, while establishing a best-fitting value of the free parameter c_x/c_y .

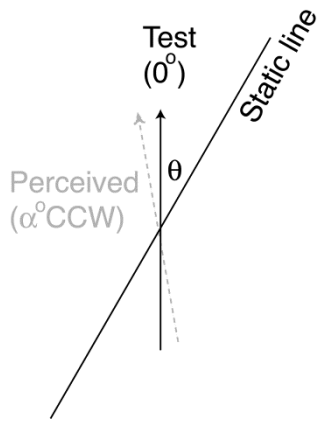


Figure 3. Schematic example of the stimulus configuration used in Experiment 1: an RDK with a static line oriented at θ° clockwise (CW) to the test direction, which is vertical (0°). The grey dotted arrow indicates the perceived direction of the test stimulus, which is α° CCW of vertical in this example. Subjects were required to indicate whether the test direction appeared to be CW or CCW of vertical. The stimulus was presented at various angles, based on subject responses, until the subject perceived the test stimulus as vertical. In this example, at the point of subjective vertical (PSV), the test direction is α° CW. Values for α were obtained for each value of θ . Note that, as the test direction is rotated, the orientation of the static line relative to the test direction (θ) remains constant.

2.1 Method

All experiments were carried out in accordance with the regulations of Macquarie University Ethics Committee and the Declaration of Helsinki.

2.1.1 Observers Seventeen psychology students at Macquarie University completed the experiment. All were inexperienced observers and none were aware of the purpose of the study. All were emmetropic or had corrected-to-normal vision.

2.1.2 Apparatus All stimuli were generated and presented and all responses recorded with Psykinematix version 1.1.0 (build 1011) (KyberVision, Montreal, Canada, psykinematix.com). The software was run on a G5 Macintosh Dual 2 GHz Power PC running Mac OS X version 10.4.11. The SONY Trinitron Multiscan G520 monitor had a frame refresh rate of 75Hz and a

pixel resolution of 1152x870. Participants viewed the screen binocularly from a distance of 57cm through a cylinder (diameter 30cm, length 57cm) that was lined internally with matte black felt. Screen borders were therefore not visible. A chin and head rest prevented head movement.

2.1.3 Stimuli A unidirectional white-on-grey RDK (test stimulus) comprising a coherently drifting set of 40 Gaussian dots was presented within an 8 deg virtual aperture with no visible boundary. All dots had a peak luminance of 104 cd/m^2 , with a standard deviation of 6 min arc and a drift speed of 0.5 deg/s. The background luminance was 65 cd/m^2 , giving a Michelson contrast of 23.1%. Dependent upon each observer's responses, the test stimulus drifted in a range of directions close to upward vertical (0°). The inducing stimulus was a static white line (length 27.78 deg, and width 0.12 deg) whose midpoint was located in the centre of the display. The luminance profile along the line's length followed a sin curve (0.018 cpd) with maximum contrast (23.1%) at the line's midpoint, decreasing to 0% contrast at each endpoint. The line was presented at one of seven orientations ($\theta = 0, 15, 30, 45, 60, 75, \text{ and } 90^\circ$). The line's orientation was yoked to the test direction, so that values of θ denoted line orientations relative to the test direction rather than to any absolute direction (positive values indicate CW directions).

2.1.4 Procedure Each trial began with a brief tone and a 0.5 s inter-stimulus interval (ISI), which consisted of a uniform grey field with a small fixation point in the centre of the screen. Test stimuli were then presented for 0.5 s, during which time the central point was not present. Observers were instructed to remain fixated as near as possible to where the point had initially been presented. Being the centre of the display, this point coincided with the midpoint of the static line. The seven test conditions were fully randomised within a single block of trials. Observers indicated, using the left and right arrow keys, which side of upward vertical (0°) they perceived the test stimulus to be moving. Observers completed two randomly interleaved 1-up-1-down staircases with respective starting values of $\pm 20^\circ$ from vertical, for each condition. Initial

step size was 32° , and was reduced by 50% on each subsequent reversal to a minimum of 1° . Each staircase terminated after 12 reversals, with the direction of the test stimulus on the final 6 reversals from each staircase being averaged for each observer to serve as an estimate of the point of subjective vertical (PSV). Because we were interested only in relative directional shifts across line orientations, no baseline measurement was necessary.

2.2 Results and discussion

The results from Experiment 1 are shown in Figure 4. Directional shifts did not occur at relative line orientations of 0 or 90° . However, intermediate orientations yielded large CCW shifts in perceived direction. A one way ANOVA produced a significant main effect of θ ($F_{(6,96)} = 20.73$, $p < 0.0005$, $\eta^2 = 0.564$). A set of one-sample two-tailed t-tests (using a Bonferroni-correction of the critical p value (0.00714) to account for multiple comparisons) showed CCW shifts significantly different from zero for each of the $\theta = 15, 30, 45, 60$ and 75° conditions ($t_{(16)} \geq 3.062$, $p \leq 0.007$) and no significant shift for the 0 and 90° conditions ($t_{(16)} \leq 1.201$, $p \geq 0.247$). The overall pattern of results very closely resembles that reported in our previous study (Farrell-Whelan, et al., 2012), where an identical stimulus configuration was used. The results are consistent with the differential processing model's qualitative prediction that the perceived direction of a stimulus moving obliquely to the orientation of a straight line will be perceptually shifted away from the line's orientation.

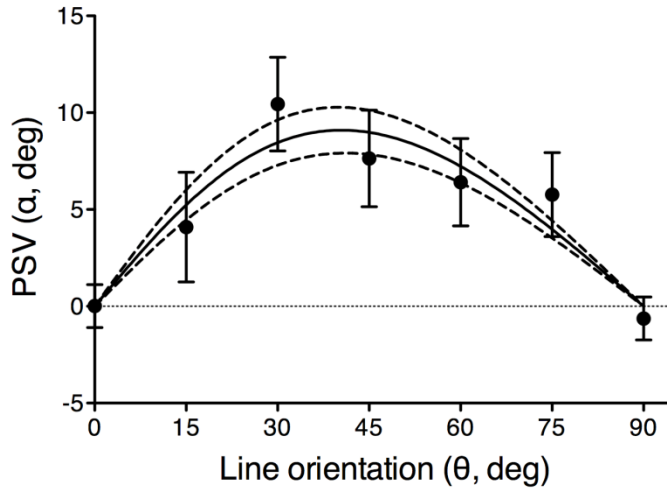


Figure 4. Graph showing the means and 95% CIs of the point of subjective vertical, or PSV (α) as a function of the orientation of the static line relative to the test direction (θ), along with model predictions, and associated 95% confidence bands.

The model's predictions of α across different values of θ are shown in Figure 4, giving an opportunity to visually assess their accuracy compared with psychophysical measurements. To assess the quantitative predictions of the formal differential processing model, an extra sum-of-squares test was employed, showing that the model provided a significantly closer fit to the data than did the null hypothesis ($F_{(1, 118)} = 230.9$, $p < 0.0001$, $R^2 = 0.402$). We obtained a best-fit value for c_x/c_y of 0.7270, with a 95% confidence interval (CI) from 0.6965 to 0.7574. The model's assertion that $c_x/c_y < 1$ and is a constant ratio was therefore supported by our findings. A replicates test could find no evidence that the model is inadequate at predicting the values obtained by psychophysical experimentation ($F = 1.846$, $p = 0.0964$).

Consideration was given to the possibility that the reported results reflect shifts in perceived vertical towards the line's orientation rather than in perceived direction away from the line's orientation. Shifts in perceived vertical due to the presence of an obliquely oriented line have been reported previously (e.g. Asch & Witkin, 1948; Li & Matin, 2005). The reported shifts

were measured by having observers judge the orientation of a vertical line. The veridically vertical test line was perceived as tilted away from the inducing line. This is the well-known tilt illusion (e.g. Wenderoth & Johnstone, 1988). The results were interpreted as a shift in perceived vertical towards the orientation of the inducing line. The current results could be interpreted the same way. However, even if the tilt illusion is attributable to a shift in perceived vertical, there are two reasons to consider such an interpretation of the current data to be very unlikely. Firstly, during foveal viewing tilt illusions are nearly an order of magnitude smaller than the SDI (Schwartz, Sejnowski, & Dayan, 2009; Wenderoth & Johnstone, 1988). Secondly, while the tilt illusion switches from a ‘repulsion’ effect at small inducer-test orientation separations ($\sim 15^\circ$) to one of ‘attraction’ at large separations ($\sim 75^\circ$) (Schwartz, et al., 2009; Wenderoth & Johnstone, 1988), the SDI remains repulsive at 75° . We can therefore discount with some confidence the interpretation that the SDI arises from an induced shift in perceived vertical.

3 Experiment 2 – Speed

Experiment 2 was designed to measure the perceived speed of the RDK in the direction in which it was perceived in Experiment 1, i.e. to measure the relative perceived speed, z'/c_y . The results are reported as the point of subjective equality (PSE) of the perceived speeds of the directionally altered stimulus (standard) and a test stimulus. For the test we used the stimulus from the 90° condition in Experiment 1 because it induced no shift in direction and because we expected that it would be perceived as faster than the stimuli across the range of remaining line orientations, thereby simplifying the interpretation of the PSE. As the line in the test stimulus is inclined at 90° , the velocity of the test stimulus has only an OR component, i.e., $\mathbf{z} = \mathbf{y}$. Thus, its perceived speed can be represented equivalently as either z' or y' . According to the model, $y' = c_y \cdot y$, so in the test stimulus $z' = c_y \cdot z$, or $z'/c_y = z$. The perceived speed of the standard can only be

determined by its PSE with the test stimulus. Thus, when the perceived speeds of the test and the standard are equal, i.e. $z'_T = z'_S$, we record a PSE of z_T . Given that $z'_T = c_y \cdot z_T$, and hence $z'_S = c_y \cdot z_T$ then the PSE that we record (z_T) actually represents z'_S/c_y . These measurements will be compared with the model's prediction that $z'/c_y = z\sqrt{((c_x/c_y)^2 \cos^2\theta + \sin^2\theta)}$.

3.1 Method

3.1.1 Observers The 17 observers who participated in Experiment 1 also participated in Experiment 2.

3.1.2 Apparatus and stimuli The apparatus was identical to that in Experiment 1, but several changes were made to the stimulus configuration. Two stimuli were employed here, termed the standard and the test. The standard was presented for 0.5 s, and the test was presented for either 0.33 or 0.67 s, being respectively 33.3% shorter or longer in duration than the standard. We used the two durations to control for the possibility that observers were basing their judgments on perceived displacement rather than on perceived speed alone. The standard dots had a drift speed of 0.5 deg/s, as in Experiment 1, while the speed of the test dots was dependent on observer responses. The test incorporated a static line oriented at 90° relative to the direction of dot motion, while the line in the standard was of one of 7 orientations (0, 15, 30, 45, 60, 75, and 90°) relative to the dot motion. The direction of the standard dots in each condition was determined by the individual observer's PSV from each of the 7 corresponding conditions in Experiment 1. The direction of the test dots was set at each observer's PSV obtained in the 90° condition only. Thus, all speed judgments were based on stimuli that were perceived as moving vertically (see Figure 5). We set the perceived direction of both standard and test to vertical to achieve maximum accuracy, since Schrater and Simoncelli (1998) reported having found that speed judgments

within a matching paradigm are less accurate when the two stimuli are seen moving in different directions.

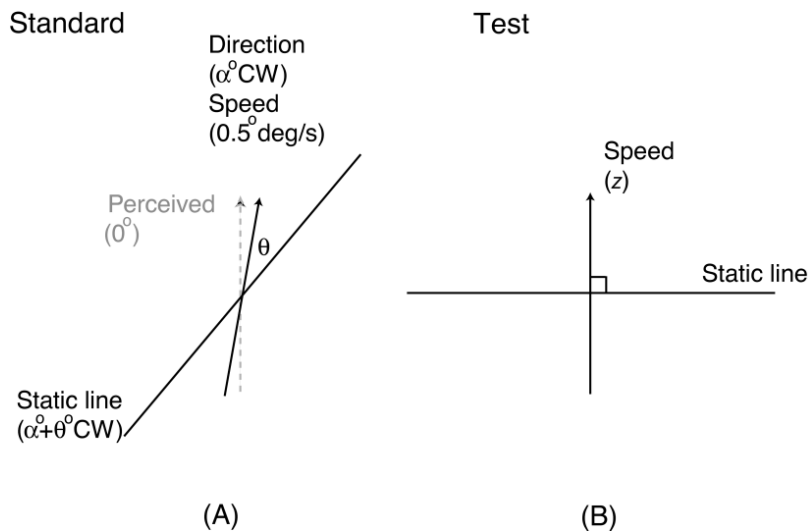


Figure 5. Schematic example of standard (A) and test (B) stimulus configurations used in Experiment 2. A sequential matching paradigm was used, whereby the observer indicated whether the test speed (z) was faster or slower than the standard speed (0.5°deg/s). The test speed was respectively decreased or increased until the point of subjective equivalence (PSE) was attained. PSV values (α) obtained for each value of θ in Experiment 1 were assigned to the standard in Experiment 2, such that the standard drift direction was perceived as vertical. The PSV value (α) obtained for the 90° condition in Experiment 1 was assigned to the test direction.

3.1.3 Procedure A 2AFC sequential matching procedure was used (see Figure 5). Each trial began with a brief tone and a 0.5 s ISI, as in Experiment 1. This was followed by the presentation, in random order, of the standard and the test, which were separated by another 0.5 s ISI. Observers were required to use the ‘z’ and ‘m’ keys to indicate whether the first or second stimulus had the greater speed. A fully randomised interleaved double 1-up, 1-down staircase was used. The test speed was initially set at 0.2°deg/s for one staircase and at 0.8°deg/s for the other. Step sizes decreased by 25% on each trial prior to the first reversal, after which step sizes decreased by 5% on each trial. Each condition terminated after 11 reversals of each staircase, and the final 6 reversals were averaged to give the PSE of the standard dots.

3.2 Results and discussion

The difference between the values obtained for the two test durations averaged over the 7 conditions was 0.009 deg/s (95% CI = 0.023). A one-way repeated-measures analysis of variance found the difference to be non-significant ($F_{(1,16)} = 0.740, p = 0.402$), nor was there a significant interaction between test duration and relative line orientation (θ) ($F_{(6,16)} = 0.674, p = 0.671$). Values for the two durations have therefore been averaged in the reported results. The graph in Figure 6 shows the means and 95% CIs of PSEs of the standard speed, i.e. z'/c_y , across the 7 relative line orientations (θ). Concordant with the qualitative predictions of the model, the perceived speed of the standard (z'/c_y) increased with increasing relative line orientations. A one-way repeated measures analysis of variance confirmed the significance of this effect ($F_{(6,11)} = 13.497, p < 0.0005$). From the speed PSE values, we calculated c_x/c_y across values of θ for each participant. An extra sum-of-squares test of the aggregate data showed that the model provided a significantly closer fit to the data than did the null hypothesis ($H_0: c_x/c_y = 1$) ($F_{(1, 118)} = 218.8, p < 0.0001, R^2 = 0.017$). We obtained a best-fit value for c_x/c_y of 0.7512, with a 95% CI from 0.7168 to 0.7856. The model's assertion that $c_x/c_y < 1$ was therefore once again supported by our findings. Although the model outperforms the null hypothesis at accounting for the data, a replicates test showed evidence that this model is inadequate at fully accounting for our perceived speed data ($F = 35.99, p < 0.0001$), as might be suspected from the relatively small values of R^2 obtained for this fit.

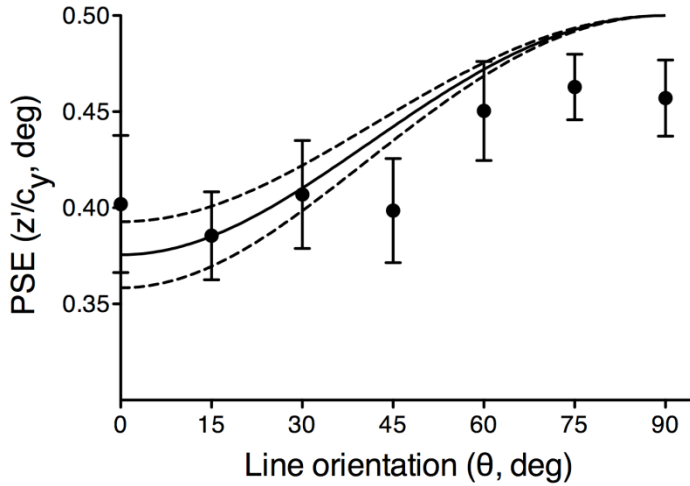


Figure 6. Graph showing mean PSEs with 95% confidence intervals, along with model predictions, using the best-fitting value of c_x/c_y (0.7512), along with 95% confidence bands across values of θ .

Comparing the best-fit values of c_x/c_y from Experiment 1 (0.7270, with a confidence interval from 0.6965 to 0.7574) and Experiment 2, the proportion of CI overlap (i.e. the CI overlap (0.0406) as a proportion of the average margin of error (0.0324) = 1.252) indicates a distinct lack of a significant difference between the value of c_x/c_y calculated from the two data sets (see Cumming & Finch, 2005).

4 General discussion

Many studies have investigated instances in which changes to an object's spatial context result in changes to its perceived velocity. In a previous study (Farrell-Whelan, et al., 2012), we found that a static line induced a shift in the perceived direction of an RDK stimulus moving obliquely to the line's orientation, which we have replicated here (Experiment 1). We proposed that the shift occurred due to the differential processing of NOR and OR component velocities, as has been proposed previously to explain shifts in perceived direction within other related stimulus configurations (e.g. Cutting & Proffitt, 1982; Duncker, 1929/1955; Johansson, 1950;

Wallach, Becklen, & Nitzberg, 1985), including the direction illusion (Dakin & Mareschal, 2000). That these qualitative predictions of differential processing are upheld supports the basic proposal that this mechanism underlies aspects of direction perception in the context of the SDI, as well as in other situations. Furthermore, this study has documented an entirely new, complementary phenomenon: that under the same circumstances, stimulus speed is also misperceived for some line orientations more than others. Again, differential processing is able to successfully predict this effect in a qualitative sense.

In an effort to provide a more stringent test of the differential processing proposal, we have developed a unified model of perceived velocity with the capacity to generate explicit quantitative predictions both of perceived direction and perceived speed across the various line angles tested. This model proposes that veridical velocity vectors are resolved into NOR and OR component velocities with the NOR component velocity being perceptually underestimated with respect to the OR component velocity by a constant ratio (i.e. $c_x/c_y < 1$). Although this model is elementary (one free parameter only), the success of its predictions was good, if not perfect. The model fit the data significantly better than the null hypothesis in the case of both direction and speed, returning best-fitting values of c_x/c_y that lie significantly below 1, as demanded by the model.

For the model to be considered successful at predicting perceived velocity in general, the ratio of the perceptual NOR-to-OR component velocities should be the same whether calculated from the direction-shift data or from measurements of corresponding shifts in perceived speed. The value of the ratio calculated from the speed data was not dissimilar to that calculated from the direction data. These findings indicate that the same unified differential processing model can successfully account for the observed velocity shifts, whether they involve misperceptions of direction or velocity. However, we also found that the model in its current formulation was not

able to fully predict the PSE values for speed, as indicated by the R^2 value and the rejection of the fit by the rather stringent replicates test. The inability of the model to perfectly account for shifts in perceived speed indicates that although perceived direction can be accounted for by differential processing, the perception of stimulus speed in the context of the SDI may involve factors external to our model as currently defined. This is perhaps not surprising in light of the many studies showing that perceived speed can be influenced by a range of different factors that do not appear to have a bearing on perceived direction, e.g. contrast (Blakemore & Snowden, 1999; Thompson, Brooks, & Hammett, 2006; Thompson, Stone, & Brooks, 1995), spatial frequency (Brooks, Morris, & Thompson, 2011; Diener, Wist, Dichgans, & Brandt, 1976; Ferrera & Wilson, 1991; Kooi, De Valois, Grosf, & De Valois, 1992; McKee, Silverman, & Nakayama, 1986) and colour (Cavanagh & Anstis, 1991; Cavanagh, Tyler, & Favreau, 1984). Nevertheless, this elementary model's relative success at making predictions of perceived speed may be seen as an achievement, given that the effect of line orientation on perceived speed is entirely novel, having never previously been documented. Although quantitative predictions of perceived speed were far from perfect, we believe that this represents an important first step in attempting to account simultaneously for misperceptions of velocity (whether it be of direction, speed, or both) with a single elementary model. Although models and theories of direction perception and speed perception abound, unified models of velocity perception are relatively rare (see Dakin & Mareschal, 2000; Weiss, Simoncelli, & Adelson, 2002 for exceptions). It should be noted that these models fare better at accounting for perceived direction than they do for perceived speed (e.g. Weiss, et al., 2002 Figure 5) even with the inclusion of additional free parameters (Dakin & Mareschal, 2000).

The results are consistent with the model's qualitative predictions insofar as the perceived velocity was found to increase with increasing relative line orientations. This finding lends

support to the model's assertion that the perceptual NOR component velocity is underestimated with respect to the perceptual OR component velocity. This is an important result, since it shows agreement with previous studies that have found NOR motion to be perceived as slower than an equivalent veridical velocity seen in OR motion (Blakemore & Snowden, 2000; Brown, 1931; Gogel & McNulty, 1983; Nguyen-Tri & Faubert, 2007; Norman, et al., 1996). However, the current findings are distinct from those of previous studies, since this study has for the first time made direct predictions of both perceived direction and speed in stimuli containing both NOR and OR velocity components. That our results find concordance with the earlier studies suggests that the processes responsible for the extraction of NOR and OR component motions may be the same as those responsible for the perception of objects translating with either OR motion only or NOR motion only.

5 Conclusion

The current paper has replicated our earlier finding (Farrell-Whelan, et al., 2012) that a static line causes the perceived direction of a moving object (RDK) to shift away from the line's orientation (the statically-induced direction illusion). This finding is consistent with the differential processing model, which contends that the illusion results from the underestimation of the component of the object's velocity parallel to the line (non-object-relative component velocity) in comparison to the component orthogonal to the line (object-relative component velocity). We have here formally defined the model using the assumption that the perceived component velocities are proportional to their respective actual velocities and that the extent of this relative underestimation is constant across the values of line angle, and hence across different underlying OR and NOR component speeds. To test the model's success as a unified account of perceived velocity, we first measured the size of the shift in perceived direction across a 90°

range of line orientations and then measured the perceived speed of each motion stimulus in its perceived direction. Both data sets yielded a ratio of perceptual non-object-relative to object-relative component speeds that could be described in accordance with the model's stipulations, i.e. the ratios were both < 1 , and were comparable to each other. Beyond its success in qualitative predictions, the model thus provides a relatively successful quantitative account of the observed shifts in direction and speed. The results therefore do not disqualify the involvement of differential processing. Rather, they indicate that the illusions described here can be attributed largely to differential processing, while the discrepancy between predicted and obtained component speed ratios may implicate the involvement of additional factors not yet captured by our model.

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5 DI and DAE processing stages

Until now, the current study has focused on establishing a model of relative motion processing to account for the effects of spatial context on perceived velocity. We have seen that a model of differential processing can account for most of the obtained data. However, the integrity of such a model must ultimately rest on the feasibility of its physiological implications. Therefore, to complement the previous findings, the final paper takes a different approach to understanding the mechanisms involved by investigating the potential neural locus or loci of the processes underlying the DI.

As noted in the introduction, cells that respond to velocity discontinuities between their CRF and surround are considered to be the neural substrate of velocity segmentation and therefore the mechanism underlying the extraction of OR motion (e.g. see Murakami & Shimojo, 1996; Shioiri et al., 2002). The scale of OR motion perception implicates the involvement of foveal V1 CRFs (e.g. Lamme, Van Dijk & Spekreijse, 1993; Murakami & Shimojo, 1996; Van Doorn & Koenderink, 1982), the large surrounds of which are likely to provide contextual information through feedback from MT (e.g. Harrison, Stephan, Rees & Friston, 2007; Sullivan & de Sa, 2006). Moreover, MT neurons are activated by large-scale, global motion, i.e. NOR motion (Allman, Miezin & McGuinness, 1990; Britten, Shadlen, Newsome & Movshon, 1992). Thus, differential processing, which involves the differential extraction of OR and NOR components, is likely to occur at multiple levels of the hierarchical neural pathway and involve complex two-way communication between these processing stages. The DI should involve similar multi-stage processing if it is to be attributed to differential processing, as the previous papers suggest.

Several studies have attempted to localise the DI's neural substrate by comparing characteristics of the illusion with those of a purportedly related phenomenon, the direction

aftereffect (DAE). The DAE is a shift in perceived direction that occurs in the test set of dots presented alone after previous adaptation to the inducing set of dots, so that it may be considered as successive rather than simultaneous repulsion (Mather & Moulden, 1980). The DAE, like the DI, has been attributed to a distribution shift, but due to adapted cell populations tuned to the adapting stimulus inhibiting responses in cells tuned to the test stimulus (Levinson & Sekuler, 1976). By comparing aspects of the DAE and the DI, it may be possible to ascertain whether they arise from different motion processing stages. It has further been proposed (Curran et al., 2009) that if separate stages are involved, then it may also be possible to determine where in the motion processing stream the processes occur in relation to each other by establishing a sequential order to the activity giving rise to the respective phenomena. If no sequential relationship does exist, this would indicate that the two stages of processing are not entirely independent. Since some previous studies attribute the DI to early processing and the DAE to a higher-level mechanism while other studies have found the reverse, if the associated processes are not sequentially independent, this might suggest that each phenomenon is associated with multiple stages of processing. As differential processing is likely to involve multi-level processing, determining whether this is true of the DI will test the feasibility of the differential processing proposition.

Curran et al. (2009) found that DI-related processing does not occur sequentially prior to that of the DAE. The main objective of the following paper is to ascertain whether DAE-related processing occurs prior to that of the DI. The paper thus focuses on one very specific aspect of the DI in an attempt to incrementally further our understanding of its neuronal underpinnings.

5.1 Manuscript 4

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The hierarchical order of processes underlying the direction illusion and the direction aftereffect

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Abstract

Motion perception involves the processing of velocity signals through several hierarchical stages of the visual cortex. To better understand this process, a number of studies have sought to localize the neural substrates of two misperceptions of motion direction, the direction illusion (DI) and the direction aftereffect (DAE). These studies have produced contradictory evidence as to the hierarchical order of the processing stages from which the respective phenomena arise. We have used a simple stimulus configuration to further investigate the sequential order of processes giving rise to the DI and DAE. To this end, we measured the two phenomena invoked in combination, and also manually parsed this combined effect into its two constituents by measuring the two phenomena individually in both possible sequential orders. Comparing the predictions made from each order to the outcome from the combined effect allowed us to test the tenability of two models: the DAE-first model and the DI-first model. Our results indicate that DAE-invoking activity does not occur earlier in the motion processing hierarchy than DI-invoking activity. Although the DI-first model is not inconsistent with our data, the possible involvement of non-sequential processing may be better able to reconcile these results with those of previous studies.

1. Introduction

Motion perception defines our spatiotemporal visual experience, although it is not always reliable. Instances in which motion is misperceived offer unique opportunities for studying the mechanisms involved in motion processing. The current paper investigates the hierarchical order of neural processes underlying two misperceptions of motion direction, the direction illusion (DI) (Marshak and Sekuler 1979; Mather and Moulden 1980) and the direction aftereffect (DAE) (Levinson and Sekuler 1976). The DI is an illusory exaggeration of the angle between the respective directions of two moving stimuli. It has often been studied using transparent motion displays, typically bidirectional random dot kinematograms (RDKs), which consist of two superimposed sets of random dots each scrolling continuously in a different direction (Figure 1). The DI is usually measured as the shift in perceived direction of one set of dots (test) due to the presence of the other set (inducer). The DAE is a shift in perceived direction that occurs in one stimulus after adaptation to another stimulus moving in a different direction, and is invoked through the successive presentation of two unidirectional RDKs (adaptor and test) (Figure 2). Thus, the DI and DAE are the results of, respectively, spatial and temporal contextual effects.

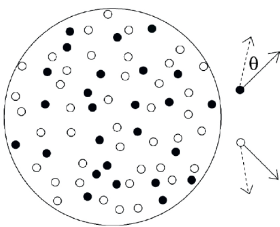


Figure 1. Schematic diagram of the direction illusion (DI): Black and white dots in the diagram represent the two random dot sets, which are both white in the actual display. Solid and dotted arrows indicate, respectively, their physical and perceived directions. Repulsion magnitude is measured as the size of the angle (θ).

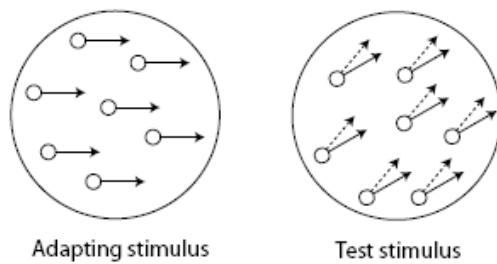


Figure 2. Schematic diagram of the direction aftereffect (DAE), showing the adapting stimulus (left) translating rightward (90°) and the test stimulus (right) translating at 60° clockwise of upward vertical (0°), as indicated by the solid arrows. Dotted arrows represent perceived direction, which is shifted angularly away from the adapting direction.

For the visual context, spatial or temporal, to influence motion perception, some level of integration of the visual scene must be taking place. Two stages of the human visual motion system hierarchy that have been implicated in motion integration are the primary visual cortex (V1) and the middle temporal area (MT). It is broadly accepted that V1 is responsible for extracting fine-grained local motion signals, first in layer $4C\alpha$, then layer 4B, which then feed into MT (Anderson et al 1998) where they are integrated to form a more global representation (Huk and Heeger 2002; Movshon and Newsome 1996; Qian et al 1994; Snowden et al 1991).

Investigations into the possible neural substrates of the DI and the DAE have yielded contradictory results. Some research has indicated that the DI may result from local motion processing early in the hierarchical motion pathway, i.e. in area V1 (Grunewald 2004; Hiris and Blake 1996; Marshak and Sekuler 1979; Wiese and Wenderoth 2007, 2010), while other studies attribute the DI to global motion processing in MT (Benton and Curran 2003; Curran et al 2009; Wilson and Kim 1994). Similarly, while some studies have suggested that the DAE results from the adaptation of early, local motion processes in V1 (Curran et al 2006, 2009), others have produced evidence that the DAE arises later from the adaptation of global motion processes in MT (Patterson and Becker 1996; Schrater and Simoncelli 1998; Wiese and Wenderoth 2007, 2010).

Evidence that the DI arises from local V1 processing comes from dichoptic studies, in which the inducer is presented to one eye and the test to the contralateral eye. These studies have shown that under such circumstances, the size of the shift in the perceived test direction is reduced to ~60% of the value observed using binocular or monocular presentation (Grunewald 2004; Marshak and Sekuler 1979; Wiese and Wenderoth 2007, 2010). Because all cells in MT respond to binocular stimulation to a greater or lesser extent, i.e. stimulation in either eye (Maunsell and van Essen 1983) while many V1 cells (in layer 4C α) respond only to monocular input (Merigan and Maunsell 1993; Poggio and Poggio 1984), the ~60% interocular transfer (IOT) suggests a V1 locus for DI-associated motion processing³. In agreement with this, Hiris and Blake (1996) reported that DI magnitudes remain unchanged whether the two dot sets are presented at different disparities or are coplanar. This has been interpreted as evidence that the substrate of the DI is found early in the motion-processing pathway (Grunewald 2004; Wiese and Wenderoth 2007). Since binocular disparity-tuned cells are found in MT (Maunsell and van Essen 1983) and in layer 4B of V1 (DeYoe and Van Essen 1985; Hubel and Livingstone 1987; Poggio and Poggio 1984), the evidence suggests an even earlier processing stage, such as layer 4C α .

Contrary to the evidence that the DI is driven by early local processing in V1, Benton and Curran (2003) have shown that the DI arises from global processing in MT. They first measured the DI in a bidirectional RDK across several inducer speeds. They also measured the DI invoked by a display consisting of a set of dots all moving at the average of these inducer speeds. They then measured the DI with a mixed-speed inducer, which consisted of all of these speeds, and

³ These results have been contested (Curran, Clifford and Benton, 2009) on the basis that the DI is also reduced during binocular rivalry (Chen, Meng and Matthews, 2005). Binocular rivalry is the involuntary alternation between two percepts when dissimilar images are presented dichoptically. However, Wiese and Wenderoth (2010) have recently shown that the IOT of the DI is reduced when induced with a centre-surround dichoptic display, which prevents binocular rivalry.

therefore contained both local and global motion signals, the local signals being those of the component speeds and the global signal being the average speed. They reasoned that, if the DI arises from local motion processing, then the size of the DI invoked by the mixed-speed inducer should correspond with the vector average of the DIs invoked by the individual speeds, but if the DI arises instead from global motion processing, then the size of the DI invoked by the mixed-speed inducer should correspond to the DI invoked by the set of dots moving at the average speed. They found the latter to be the case. Patterson and Becker (1996) have shown that the DI can be invoked in a cyclopean display, in which the drifting dots are defined purely by binocular disparity and are not monocularly visible. Since binocular disparity-tuned cells are only found beyond layer 4C α of V1 (see Born and Bradley 2005), this implies that the neural substrate of the DI also lies beyond this stage, possibly in MT.

The DAE, like the DI, has been attributed by some to early local motion processing in V1 and by others to later global motion processing in MT. Curran et al. (2006) have provided evidence that the DAE stems from local motion processing, indicating an early V1 substrate. Using a mixed-speed stimulus, similar to that with which they tested the DI, but this time as an adaptor, they showed that the size of the DAE is determined by the adaptor's local component speeds and not by its global average speed. Curran et al. (2006) produced further evidence that the DAE is driven by local V1 adaptation by showing that the size of the shift in the perceived test direction is reduced to ~70% when the DAE adaptor is presented to the eye contralateral to the test stimulus.

Contradicting Curran et al.'s (2006) results, Wiese and Wenderoth (2007) found the DAE to exhibit 100% IOT, indicating that it arises from binocular processing at least beyond layer 4C α of V1, possibly in MT. Also in support of an MT locus of the DAE, Patterson and Becker (1996) found, as they did with the DI, that the DAE could be invoked in a cyclopean display where no

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monocular figures are visible. In a second experiment, they also found that a cyclopean adaptor could invoke a DAE in a luminance-defined test stimulus, and vice versa. Because the DAE transfers across stereoscopic and luminance domains, their substrates must overlap substantially, suggesting that each of these effects is mediated by higher cortical areas involving substantial binocular processing, such as MT. Further evidence that the DAE arises from global motion processing in MT comes from Schrater and Simoncelli (1998). In one experiment, they measured the DAE using a grating stimulus as the adaptor and a plaid (two superimposed component gratings with different orientations) as the test. While isolated gratings present only local “component” motion signals that are processed in V1, the global motion percept of plaid direction is signalled by “pattern” cells in MT (Movshon et al 1985). The test stimulus was configured in such a way that its perceived direction would be shifted towards or away from the adaptor depending on whether the DAE was operating at the local or global stage. They found the latter to be true.

Curran et al. (2009) conducted a study to test for evidence that the DI and DAE arise from different motion processing stages and to investigate where in the motion processing pathway these stages might lie. To this end, they set out to establish whether there is a sequential order in which the two phenomena arise and, if so, what that order is. Curran et al. (2009) (Experiment 1) used a bidirectional mixed-speed RDK adaptor, wherein fast and slow (7 and 2 deg/s) motion components moved in directions 25° either side of vertical. They subsequently measured the DAE with a unidirectional (vertical) mixed-speed (fast and slow) RDK test. They showed that the fast motion component of the test was directionally shifted away from the fast adaptor component and the slow test component was directionally shifted away from the slow adaptor component, resulting in the unidirectional test RDK being perceived as bidirectional. Further, they found that the magnitude of the perceived separation of the test stimulus components was not consistent

with the DAE alone, but could be accounted for by the presence of a DI also arising within the perceptually bidirectional test stimulus. Note that the DAE could not have arisen after the DI, since without the DAE the test stimulus would have remained unidirectional. The results suggest that the DI does not arise from an earlier stage of processing than the DAE. In the same experiment, Curran et al. (2009) measured the DAE in both a 2deg/s and a 7deg/s single-speed test to obtain an estimate of the bidirectional DAE without the 'subsequent' DI also occurring. They then measured the DI with test and inducer directions determined by the obtained single-speed DAE values. They found that the combined bidirectional DAE and DI was of the same size as the separate DAE and DI shifts combined in a simple linear addition.

In a second experiment, Curran et al. combined DI- and DAE-invoking stimuli in such a way that the perceived test direction would be shifted either away from or towards the adapting direction, depending on the order in which the two processes occur in the visual system (Figure 3). Participants adapted to a bidirectional RDK that invoked a DI. They were then presented with a unidirectional RDK test with a direction midway between one of the actual adapting directions (a1) and its DI-induced perceived adapting direction (p1). The resulting DAE was a shift away from the actual adapting direction rather than from the perceived adapting direction, implying adaptation to the actual adaptor directions and not to the perceived adaptor directions. Curran et al. (2009) concluded that DAE-invoking adaptation was occurring at a processing stage that preceded DI-invoking processes, and that this in turn, when combined with the evidence that the DAE arises from local motion processing and the DI from global motion processing (Benton and Curran 2003; Curran et al 2006), implies that the neural substrate of the DAE is located within V1 while the DI is driven by processes within MT.

The accumulated evidence from the investigations into the neural loci of the DI and DAE outlined above is thus inconclusive. Importantly, however, the majority of studies that have

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investigated and compared these phenomena within the same paradigm (e.g. Benton and Curran 2003; Curran et al 2006, 2009; Wiese and Wenderoth 2007) indicate that they do at least exhibit different characteristics and are therefore likely to arise from largely separate processing sites.

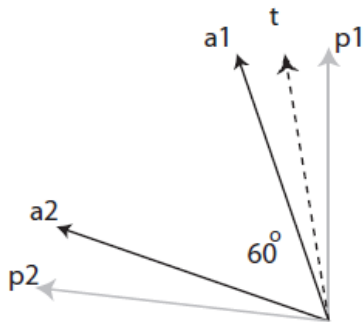


Figure 3. Vector diagram from Curran et al. (2009) showing actual adaptor directions (a1 and a2), separated by 60°, perceived adaptor directions (p1 and p2), and the test direction (t), which was midway between the nearest actual (a1) and perceived (p1) directions.

Adopting a similar strategy to that of Curran et al.'s (2009) Experiment 2, but employing different stimuli, the current study sought to compare the tenability of two models, one contending that the neural activity underlying the DI occurs prior to that underlying the DAE (DI-first model) (Figure 4A) and the other that the neural processes underlying the DAE operate prior to those underlying the DI (DAE-first model) (Figure 4B). Implicit to both models is that the outputs of the two processing stages combine additively, as reported by Curran et al. (2009). In the strictly sequential models tested here, where all processing relevant to the effect (DI or DAE) in stage 1 is entirely complete prior to any processing leading to the effect in stage 2, this is the only logical possibility. Our objective, therefore, was to attempt to discount the possibility either that DI-related processing precedes DAE-related processing in a linearly additive fashion or that

DAE-related processing precedes DI-related processing in a linearly additive fashion⁴. We approached our objective by measuring the DI and DAE in combination, i.e. as they are experienced simultaneously. We also measured the two phenomena separately in the two possible sequential orders that their processing could be occurring. To test the DI-first model, we measured the DI followed by the DAE, and to test the DAE-first model, we measured the DAE followed by the DI. For each, the test stimulus direction used in the second measurement was determined by the value obtained in the first measurement. We thus “manually” combined the outputs of the DI- and DAE-invoking processing stages sequentially to obtain predictions that could be compared to the outcome of the two phenomena arising in combination. We reasoned that, if there is a particular sequential order to the processes underlying the two phenomena, then one of our sequential measurements should produce a result that is similar to that obtained when the two are invoked in combination.

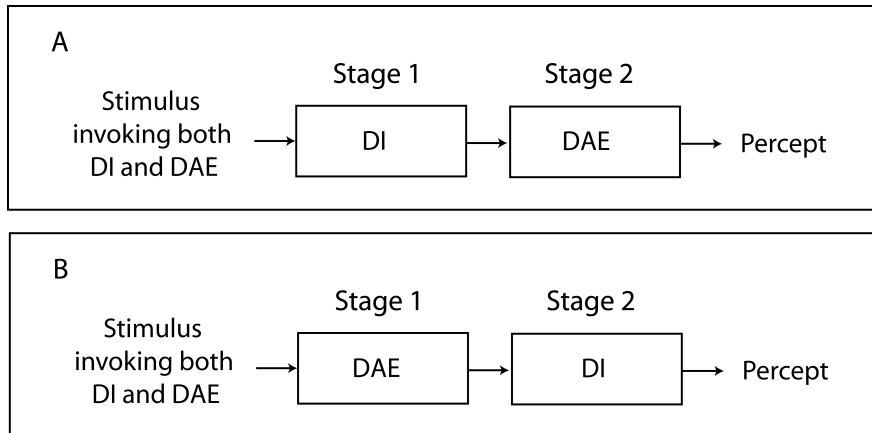


Figure 4. The DI-first and the DAE-first models. A stimulus that invokes both a DI and a DAE generates a percept that represents the resultant of the summing of the outputs of two stages of processing. A. In the DI-first model, the neural processes responsible for the DI (labelled ‘DI’, in the interests of brevity) operate at Stage 1 and those responsible for the DAE (labelled ‘DAE’) operate at Stage 2. B. The DAE-first model dictates that DAE-generating activity occurs first, at Stage 1, and that DI-producing activity occurs at Stage 2.

⁴ Hereafter, the term ‘sequential’ will also imply linear additivity.

2. Experiment 1

The first experiment was designed to measure the DI and DAE individually, as well as the effect of the DI and DAE operating in combination. We labelled the 3 respective conditions DI₁, DAE₁, and Combined (Figure 5).








Stimulus configuration		
Condition	Adaptation	Test
DAE ₁	Adaptor -90° 	Test 0°  Perceived
DI ₁	No adaptation	Test 0°  Inducer 90°  Perceived
Combined	Adaptor -90° 	Test 0°  Inducer 90°  Perceived

Figure 5. Stimulus conditions in Experiment 1. In the DAE₁ and Combined conditions, the 0° test stimulus was preceded by a -90° (90°) adaptor. In the DI₁ and Combined conditions, the test stimulus and 90° (-90°) inducer were presented simultaneously. While the actual experiment was counterbalanced with an equal number of CW- and CCW-oriented displays, shown here are the CW-oriented displays only, in which the DAE adaptor is at -90° and the DI inducer is at 90°.

2.1. Method

2.1.1. Apparatus All stimuli were generated and all responses recorded with Vpixx v2.3 (VPixx Technologies Inc., Longueuil, Canada, www.vpixx.com). The software was run on a

G5 Macintosh Dual 2 GHz Power PC running Mac OS X version 10.4.11. The SONY Trinitron Multiscan G520 monitor had a frame refresh rate of 75 Hz and a pixel resolution of 1152x870. Participants viewed the screen binocularly from a distance of 57cm through a cylinder (diameter 33cm, length 57cm) that was lined internally with matte-black felt, and a chin and head rest prevented head movement.

2.1.2. Stimuli Stimuli consisted of either a unidirectional or bidirectional white-on-black RDK (dot diameter 0.08 deg, lifetime 0.7 s, density 4 dots/deg² for each direction) within a circular aperture subtending 8 deg, which was centred on a red fixation point (diameter 0.15 deg) in the middle of the screen. Each set of dots translated coherently in a given direction at 2.5 deg/s.

The DI inducing stimulus and the DAE adapting stimulus drifted horizontally either leftward (-90°) or rightward (90°), with positive values indicating directions CW of upward vertical. The test stimulus drifted vertically upward (0°). Combining the two stimuli to measure the combined effect of the DI and DAE involved the presentation of the -90° DAE adaptor followed by the presentation of the 0° test together with the 90° DI inducer (see Figure 5).

In the DAE₁ and Combined conditions, the initial adaptation period was 60 s, followed by a 500 ms inter-stimulus grey mask and a tone to signal the beginning of the block of test trials. Trials were interspersed with 5 s top-up adaptation periods. The test stimulus was presented for 0.7 s. In the DI₁ conditions, the test and inducing stimuli were presented simultaneously for 0.7 s. In all conditions, at the offset of the stimulus a pointer appeared, occupying the same central aperture.

2.1.3. Participants Eight participants, 4 male and 4 female, were tested. Five were psychology students at Macquarie University, one was a staff member, and two were not

affiliated with the university. Two of the participants were aware of the aims of the study. All were emmetropic or had corrected-to-normal vision.

2.1.4. Procedure Instructions, a demonstration, and a block of practice trials preceded testing. For each trial, participants were required to judge the direction of the test stimulus. For DI conditions, participants were instructed as to which set of dots they were to judge. Participants responded to a subsequently presented pointer, which was initially set at either $\pm 15^\circ$ of the vertical RDK drift direction. Left and right arrow key presses resulted in the orientation of the pointer being shifted in the subsequent trial either CCW or CW, as determined by an adaptive staircase routine.

A fully randomised interleaved double staircase was used, and measurements were counterbalanced with an equal number of trials conducted with a CW-oriented display (as depicted in Figure 5) and CCW-oriented display. The CCW display reflected the CW display about the vertical axis. CW and CCW trials were conducted in separate blocks, and values were later combined for graphical representation and are reported as a single value measured in degrees CW of upward vertical, as if all conditions were CW. Since CW and CCW measurements were counterbalanced, no baseline adjustment was necessary. Step sizes for each reversal were 8, 6, 4, 2, and 1° thereafter. Each condition was terminated after 10 reversals or a maximum of 30 trials, with the mean of the final 6 reversals from each staircase averaged to give the estimated perceived direction.

2.2. Results and discussion

Results from Experiment 1 are presented in Figure 6. We obtained a mean DAE of 7.25° , a mean DI of -14.42° , and a mean combined effect of -2.52° . One-sample two-tailed t-tests

showed a significant difference from zero for each of the DAE₁ ($t(7) = 4.51$, $p = 0.003$, $\eta^2 = 0.744$) and DI₁ ($t(7) = -4.66$, $p = 0.002$, $\eta^2 = 0.756$) conditions.

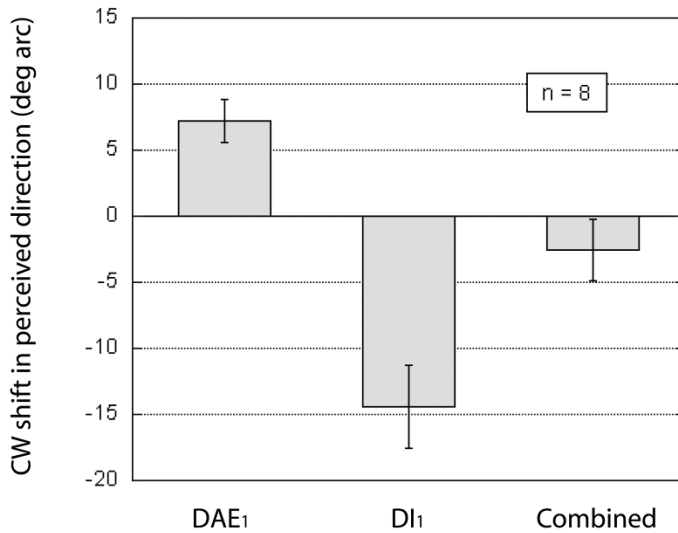


Figure 6. Graph showing the results of Experiment 1. Error bars represent +/- 1 SE.

That the DI₁ condition produced a significant effect was expected since the DI occurs up to and beyond inducer-test directional differences of 90° (Dakin and Mareschal 2000). The DAE₁ condition also yielded a significant, though smaller effect. This finding is in general agreement with previous DAE measurements with adaptor-test directional differences of 90° (Patterson and Becker 1996; Schrater and Simoncelli 1998; Wiese and Wenderoth 2007). It should be noted that the value obtained in the Combined condition is not comparable to a sum of the DI₁ and DAE₁ values, since the two phenomena have not been measured in sequence. Measuring the final outcome of the two processing stages in sequence involves first measuring the directional shift due to the first phenomenon and then using the obtained value as the initial direction of the test

stimulus in the configuration used to invoke the second phenomenon. Thus, in Experiment 2, the direction of the test stimulus in each condition was determined by the shift measurement obtained in the appropriate condition in Experiment 1.

3. Experiment 2

In Experiment 1, we obtained measurements DAE_1 and DI_1 for the respective effects when using a vertical test stimulus. In Experiment 2, we manually combined the output of DI-related processes (DI_2 condition) with the prior output of DAE-invoking processes (DAE_1), and we manually combined the output of DAE-generating processes (DAE_2 condition) with the prior output of DI-invoking processes (DI_1) to obtain respective predictions based on the DAE-first and DI-first models for the Combined condition data from Experiment 1. To this end, in the DAE_2 condition, the test direction for each participant was set to the respective perceived test direction obtained from the DI_1 condition, and in the DI_2 condition, the test direction for each participant was set to the respective perceived test direction obtained from DAE_1 (Figure 7). The predictions that would be made by the DAE-first model can therefore be expressed as the sum, DAE_1+DI_2 , and the DI-first model as DI_1+DAE_2 .



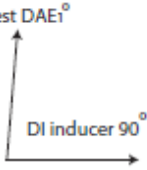
Stimulus configuration		
Condition	Adaptation	Test
DAE ₂	DAE adaptor -90° 	Test DI ₁ ° 
DI ₂	No adaptation	Test DAE ₁ ° 

Figure 7. Stimulus conditions in Experiment 2. DI₂ inducing direction = 90° (-90°), and test direction = DAE₁ value; DAE₂ adapting direction = -90° (90°), and test direction = DI₁ value. While the actual experiment was counterbalanced with an equal number of CW- and CCW-oriented displays, only CW-oriented displays are shown here, in which the DAE adaptor is at -90° and the DI inducer is at 90°.

3.1. Method

The participants, apparatus and stimuli in Experiment 2 were identical to those in Experiment 1, with two exceptions: the test stimulus directions were determined by DAE₁ and DI₁ measurements for each individual and for each direction (CW and CCW) in Experiment 1, and the Combined condition was omitted. As with Experiment 1, CW and CCW results were later combined for graphical representation.

3.2. Results and discussion

The results from Experiment 2 are shown in Figure 8. The DAE₂ and DI₂ conditions yielded respective shifts of 7.48° and -14.47°. One-sample two-tailed t-tests showed significant effects for the DAE₂ ($t(7) = 3.30$, $p = 0.013$, $\eta^2 = 0.609$), and DI₂ ($t(7) = -6.27$, $p < 0.0005$, $\eta^2 = 0.849$) conditions.

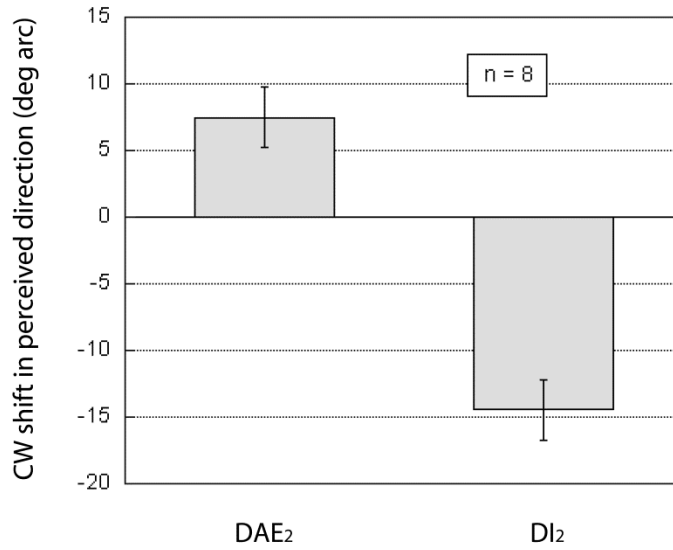


Figure 8. Graph showing the results of Experiment 2. Error bars represent +/- 1 SE.

Figure 9 shows the final predictions of the DAE-first and DI-first models, and the Combined result from Experiment 1. The final result of the DAE-first model is given by the sum, $DAE_1 + DI_2$, and the final result of the DI-first model is given by the sum, $DI_1 + DAE_2$. It should be emphasised that the calculations were made using values obtained for each individual. Having obtained measurements of the DI and DAE in the two possible sequential orders in which their respective underlying processes may occur, we were able to compare each prediction to that obtained with the two phenomena being invoked in combination. Paired two-tailed t-tests showed a significant difference between $DAE_1 + DI_2$ and Combined ($t(7) = 3.359$, $p = 0.012$, $\eta^2 = 0.617$) but no significant difference between $DI_1 + DAE_2$ and Combined ($t(7) = 1.405$, $p = 0.203$, $\eta^2 = 0.220$) (critical α was Bonferroni-adjusted to control the experiment-wise error rate).

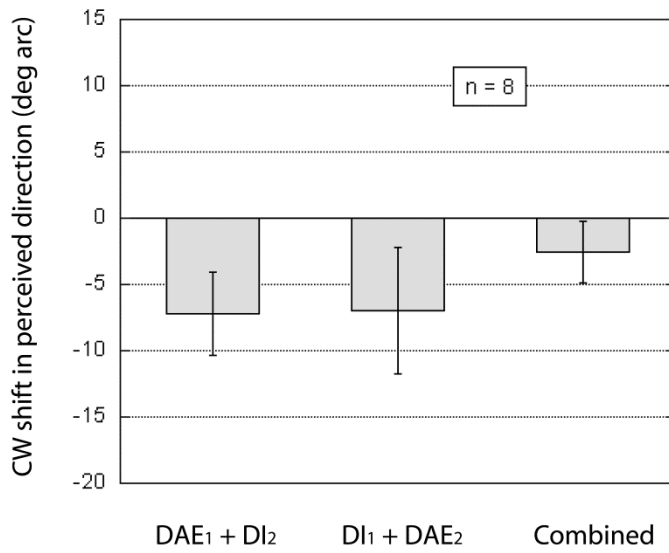


Figure 9. Graph showing the mean Combined value from Experiment 1 (-2.52°) and the predictions made by the DAE-first and DI-first models. Error bars represent ± 1 SE.

Hence, we found that the prediction made by measuring the DAE followed by the corresponding DI (DAE-first model) was dissimilar to the result of the two measured in combination. The additive DAE-first model can therefore be rejected, and we may conclude that DAE-invoking neural activity does not arise sequentially earlier than DI-invoking processes. On the other hand, we found that the prediction made by measuring the DI followed by the corresponding DAE (DI-first model) was not dissimilar to that of the two measured in combination, and hence we cannot discount the additive model in which the DI arises from sequentially earlier processing than that of the DAE.

4. General discussion

The current experiments employed a two-stage process analogous to the possible sequential neural processing underlying the DI and the DAE. Manually parsing the combined effect of the DI and DAE into its two constituents by measuring the two phenomena individually in both possible sequential orders in which their underlying processes may occur allowed us to test the tenability of two models: the DAE-first model and the DI-first model. Having found that the DAE-first prediction was dissimilar to the result obtained when the phenomena were combined, but that the DI-first prediction was not, we have rejected the DAE-first model but failed to reject the DI-first model. We may conclude from these results that the effect of the DI and DAE operating in combination is not the result of DAE-invoking activity occurring at a sequentially earlier stage of motion processing than DI-invoking activity. A distinction should be made here for the sake of clarity. The finding that the DAE does not arise from sequentially earlier processing than the DI does not necessarily imply that the DI arises from sequentially earlier processing than the DAE. In fact, we cannot assume that the combined effect is necessarily the result of the DI arising from a sequentially earlier stage of motion processing than the DAE, since we must also consider the possibility that the two phenomena combine non-sequentially.

4.1. Conflict and consonance with earlier findings

Our results are substantially consistent with many of the studies reviewed in the introduction. However, given the fact that this body of literature already presents contradictory findings, it is inevitable that our results must conflict with at least some. If we consider the possibility that the DI arises from an earlier processing stage than the DAE, then in the tradition of the antecedent literature, we might infer that the DI is likely to arise from local motion

processing within V1 and that the DAE is likely to arise from global motion processing in MT. Many of the studies described in the introduction have produced results that are consistent with this conclusion, notably those that attribute the DI to processing in V1 (Grunewald 2004; Hiris and Blake 1996; Marshak and Sekuler 1979; Wiese and Wenderoth 2007, 2010), and those that attribute the DAE to the adaptation of MT cells (Patterson and Becker 1996; Schrater and Simoncelli 1998; Wiese and Wenderoth 2007, 2010). However, as we have seen, there is also evidence that places the respective neural substrates of the DI and the DAE in MT and in V1, respectively (Benton and Curran 2003; Curran et al 2006, 2009; Wilson and Kim 1994). Of particular relevance to the current study are the findings of Curran et al. (2009) who, like us, have investigated the possible sequential order of the processes underlying the DI and DAE. In their first experiment, Curran et al. found that the DAE does not arise from a later stage than the DI. Rather than assuming at that point that DAE-related activity must therefore sequentially precede that of the DI, they acknowledged that the two phenomena may result from non-sequential “iterative processing occurring within a single neuronal population” (Curran et al 2009) within the motion processing hierarchy. As described in our introduction, the DAE observed in their second experiment corresponded to adaptation to the actual adaptor directions and not to the perceived adaptor directions, and from this they made the further, more definitive claim that DAE-related processing does in fact occur sequentially earlier than DI-related processing. Since our data indicate that the DAE does not arise from sequentially earlier processing than the DI, we must attempt to reconcile our own finding with that of Curran et al. (2009).

4.2. Reconciliation of findings

One way to reconcile Curran et al.’s (2009) results with our own is to attribute the discrepancy to differences in the stimuli employed. Curran et al. used bidirectional RDK adapting

stimuli, which thereby differed from ours, and from those used traditionally in DAE studies. Our own stimulus presents one potential confound, since the -90° DAE adaptor may perceptually alter the subsequently presented 90° DI inducer. Past investigations have found no DAE when the adaptor and test stimuli are separated by 180° (e.g. Levinson and Sekuler 1976), so the DAE adaptor should have had no directional effect on the DI inducer. However, other studies have produced results that suggest that the DAE adaptor may have affected the DI inducer's perceived speed. The velocity aftereffect (VAE) is the change in perceived speed of a test stimulus following adaptation to motion in the same or opposite direction. When the test direction is opposite that of a same-speed adaptor, its velocity has been found to increase slightly (Scott et al 1963), to be unaffected (Schrater and Simoncelli 1998), to be variably affected (Rapoport 1964), and to decrease slightly (Carlson 1962; Smith 1985; Thompson 1981). The possible occurrence of the VAE might be considered problematic, since the DI has been found to be speed tuned, with the largest shifts in perceived direction occurring with inducer-test speed ratios of between 1:1 and 3:1 (Curran and Benton 2003; Dakin and Mareschal 2000; Lindsey 2001; Marshak and Sekuler 1979). However, the VAE studies mentioned above found the effect to be very small, and its impact on our data is likely to be negligible. There are also possible confounds introduced by a bidirectional DAE adaptor such as that employed by Curran et al. (2009), since the influence of the second adapting direction is unknown. While it may possibly have confounded the findings of their first experiment, it is unlikely to have altered the findings of their second, since it differed from the test direction by $\sim 65^\circ$, at which point the DAE has been shown to be of negligible size (e.g. Wiese and Wenderoth 2007). Our results cannot therefore be reconciled with those of Curran et al. by attributing the discrepant findings simply to differences in the display. Alternatively, there is a possibility that Curran et al.'s Experiment 2 finding results from non-sequential processing. If the combined effect of the DI and DAE were arising through parallel

channels, for example, then the processes invoking the DAE would be independent of those invoking the DI, and vice versa. In Curran et al.'s experiment, both phenomena would therefore have been invoked by the actual adaptor directions, producing the same result. Attributing the combined effect of the DI and the DAE to non-sequential processing therefore reconciles the findings of the current study with those of Curran et al. (2009).

4.3. Multilevel processing

In line with this suggestion, discrepancies throughout the literature have led some authors (e.g. Wiese and Wenderoth 2010) to propose that the DI and the DAE each arise from activity at multiple processing stages. As described in the introduction, both phenomena have been found to exhibit characteristics of both local and global processing in different situations. With the exception of one directly contradictory finding, that the DAE shows both 100% IOT (Wiese and Wenderoth 2007) and ~70% IOT (Curran et al 2006), the apparent disagreement in the DI and DAE literature is resolved once the phenomena are attributed to multilevel processes. If it is the case that both V1 and MT processing are involved in generating both the DI and the DAE, this would preclude the possibility that the two phenomena arise from sequential processing.

4.4. Recurrent processing

A further complicating factor is the well-documented involvement of recurrent processing, the feedback of signals from higher to lower processing stages, in the visual integration hierarchy (see Lamme and Roelfsema 2000). Feedback signals from MT to V1 have been shown to contribute to the perception of coherent motion stimuli (Harrison et al 2007). Since the DAE is invoked by the presentation of coherent unidirectional motion, it is likely to arise from adaptation of cells involved in such feedback loops. The DI is invoked by a bidirectional stimulus, with its two components moving relative to one another. From recordings

of single- and multi-cell responses in macaque V1, the inactivation of MT has been shown to decrease V1 responses to relative motion (Hupe et al 1998). There is thus a further possible role for recurrent processing in the occurrence of the DI. Using transcranial magnetic stimulation (TMS), Silvanto, Lavie, and Walsh (2005) have found that V1 activity associated with the perceptual awareness of motion occurs both prior to and following MT activation. The involvement of multilevel, recurrent processing would not only preclude the possibility that the DI and DAE combine sequentially; it would also confound any correspondence between the temporal and structural hierarchies within the motion processing pathway. Thus, even if the DI and DAE were due to sequentially independent processing, by establishing the sequential order in which they arise we would not be able to infer the hierarchical order of their substrates. Multilevel recurrent processing may offer a very plausible reconciliation of the seemingly contradictory findings throughout the DI and DAE literature. Such processes would be likely to introduce substantial non-linearities in the combination of the DI and DAE effects that might be revealed by further testing using a larger range of stimulus parameters than were employed in this study. However, formulating a model that reflects the complexities that such processing introduces is beyond the scope of the current paper.

4.5. Conclusion

We have shown that the DAE does not arise from neural activity at a sequentially earlier processing stage than DI-related activity. This has not been previously demonstrated. Our finding is an important one, particularly in light of Curran et al.'s (2009) finding that DI-related processing does not occur sequentially prior to that of the DAE. Together our studies cast doubt on the likelihood that the two phenomena arise from sequentially independent processing and, thereby, lend credence to a multilevel processing model. The conclusion that the DI and DAE are

likely to arise from non-sequential neural processing stages takes into consideration the complexities introduced by recurrent, multilevel processing and resolves much of the disagreement in the literature regarding the processing stages that underlie the two phenomena.

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6 General discussion

6.1 Summary of findings

No study to date has reported the angular function of induced motion. The induced motion experiments included here (Chapter 2) were designed to do just this, and to thereby test the tenability of the differential processing account of this phenomenon. The differential processing account equates induced motion with the underestimation of inducer speed. It was predicted, accordingly, that across different test-inducer direction separations, if the inducer speed was kept constant the induced motion component would also remain constant. This was found to be the case, and given a constant induced motion component value, direction shifts could be predicted using simple vector summation. The geometric constraints imposed by the differential processing account dictate that, given induced motion values within an expected range, the largest shifts would occur at small test-inducer separations of $\sim 30^\circ$, similar to the peak effect found in DI studies (e.g. Wiese & Wenderoth, 2007). This too was verified by the current experiments, which showed that the entire angular function of the induced direction shifts resembled that of the DI, suggesting that the two phenomena may arise from similar processes. The second induced motion experiment investigated the effects of test and inducer speeds on the perceived test direction. The differential processing account contends that induced motion increases as a constant proportion of inducer speed, although this is likely to be true only within a limited range of speeds since induced motion has been found to be speed tuned. Therefore, if direction shifts result from the vector summation of the induced motion and veridical test motion, then the direction shift should increase as the inducer speed is increased. However, if the test speed is also increased such that the test-to-inducer speed ratio is kept constant, the direction shift should also remain constant. Therefore, according to the differential processing account, the shift in perceived direction is determined by the relative speeds of test and inducer. The results showed

that direction shift size was indeed determined by the ratio of test-to-inducer speed, with larger effects occurring when this ratio was smallest, and no effect of absolute test or inducer speed was observed. Due to the geometrical constraints associated with differential processing, it was further expected that as inducer speed is increased relative to the test speed, the peak in the angular function should occur at ever smaller test-inducer direction separations. Again, this prediction was confirmed by the data. All results reported in Chapter 2 could be summarised by a vectorial model based on the differential processing account of induced motion. The study found that the size of the induced motion component in the test trajectory was in constant proportion (k) to the speed of the inducer across all conditions, although the value of k differed across experiments, probably due to configurational differences between stimuli.

The second paper (Chapter 3) investigated further the capacity for a relative motion model based on the differential processing of NOR and OR component velocities to explain context-dependent velocity perception. The study compared two main theoretical accounts of the DI, the differential processing account and the distribution-shift account. The latter has been the more commonly accepted, and contends that the perceptual overestimation of the angle between the directions of two transparently moving fields of dots results from response distribution shifts in the populations of cells tuned to the two veridical directions. The distribution-shift account has also been applied to static orientation-shift illusions, such as the tilt illusion (Blakemore, Carpenter, & Georgeson, 1970), and to illusions arising from configurations incorporating both an orientation and a directional element (Nihei, 1973, 1975; Swanston, 1984), where motion streaks are thought to provide a basis for interactions between the two domains (Geisler, 1999; Khuu, 2012; Khuu & Kim, 2013). A novel stimulus configuration incorporating a static line aligned with the respective NOR and OR component velocities of a bidirectional RDK was used to show that the DI cannot be attributed solely to mutual inhibition between direction-selective

channels, and that differential processing provides the more plausible explanation. The study found that a static line was also effective in inducing robust changes in the perceived direction of an oblique unidirectional motion, demonstrating a new direction illusion, the SDI. The SDI stimulus configuration partly resembles those introduced by Nihei (1973, 1975) and Swanston (1984), but while they used a small dot and measured directional shifts of $\sim 2^\circ$, the RDK used here produced an effect more than an order of magnitude larger, which more closely resembles the results from other DI studies. It was further shown that the SDI could not be attributed to an interaction in the orientation domain due to the occurrence of motion streaks, since it was observed under conditions that would not normally produce motion streaks. A secondary finding of the study was that the SDI, like the DI, increased in size with decreasing RDK speed.

The occurrence of the SDI is thus more readily accounted for by differential processing than by a distribution shift, but it tells us nothing quantitative about the perceived velocity, nor of the perceptual NOR and OR component speeds, only that the NOR component speed is underestimated with respect to the OR component speed. To test the validity of the differential processing account further therefore required a more formally defined model that could be more stringently tested with measurements of both shifts in perceived direction and in perceived speed. In Chapter 4, the differential processing model was formally defined, allowing quantitative predictions to be made regarding both perceived direction and perceived speed. In the first experiment, the size of the SDI was measured across angular test-inducer separations. The model's quantitative predictions of perceived direction were confirmed. In the second experiment, perceived relative speeds across the same angular separations were measured to test the model's predictions, which were based on its predictions of perceptual component speed ratios. While the observed relative speeds followed a pattern predicted by the model, the differences across the range of separations was quantitatively smaller than those predicted. The

findings indicate that while the differential processing model captures the qualitative characteristics of perceived velocity with some success, the model as formally defined in the paper will need to be expanded before it can make successful quantitative predictions.

The previous three manuscripts have been concerned with identifying functional characteristics of the mechanism underlying context-determined velocity perception with the aim of establishing a model of relative motion processing. Two of these (Manuscripts 2 and 3) have together provided compelling evidence that the differential processing model, once improved, will account for the DI. To complement these studies, the final paper (Chapter 5) has taken a different approach, aiming instead to elucidate aspects of the neural mechanisms involved in producing the DI. Past studies that have attempted to localise the DI's neural substrate have yielded varied results, leading some researchers to propose the involvement of multi-level processes (Wiese & Wenderoth, 2010). Concordant with this proposal, since relative motion studies indicate that the extraction of NOR and OR component velocities most likely involves processing at multiple stages, the differential processing account of the DI also implicates a multi-stage neural correlate.

A study by Curran et al. (2009) found that DI-related processing does not occur sequentially prior to that of the DAE. This suggests either that the DI arises from later processing stages than the DAE or that the two phenomena do not arise from sequential stages of processing. It was therefore important to ascertain whether DAE-related processing occurs prior to that of the DI, since we would have to conclude from such a finding that the DI does result from higher level processing. However, if this were found not to be the case, then the most parsimonious conclusion would be that the two arise from non-sequential processing, and therefore possibly from multiple processing stages. The paper thus focuses on one very specific aspect of the DI in an attempt to incrementally further our understanding of its neuronal underpinnings.

The experiments in the final manuscript (Chapter 5) were designed to investigate the hierarchical order of neural processes underlying the DI and the DAE. The two phenomena were measured both as they arise in combination from a single stimulus and individually in both possible sequential orders. Comparing the predictions made from each sequential order to the outcome from the combined effect indicated that DAE-producing activity does not occur earlier in the motion processing hierarchy than that underlying the DI. This finding, in conjunction with previously existing evidence that DI-related processing does not precede DAE-related processing, suggests that the two phenomena do not arise from distinct hierarchically sequential processing sites. Moreover, the results, together with evidence from previous studies that places the DI's neural substrate respectively at different stages of the motion processing hierarchy, indicate the involvement of multi-stage, possibly recurrent, processing. Differential processing, which involves the differential extraction of NOR and OR components, is likely to span multiple levels of the hierarchical neural pathway and involve complex two-way communication between these processing stages. The current findings are therefore consistent with the differential processing account of the DI, and the neural mechanisms purportedly involved the extraction of NOR and OR component velocities provide a tenable neural framework for the processes involved in producing the phenomenon.

6.2 Theoretical and neurophysiological implications

Perhaps the most innovative empirical finding from these studies is the evidence for the occurrence of the dissociation of component velocities, as proposed by Johansson (1950). Evidence that NOR velocity is underestimated with respect to OR velocity has been documented previously, as discussed in the introduction. Studies have also described Johansson-type phenomena in terms of component dissociation. However, no study until now has produced quantitative evidence for the differential extraction of NOR and OR component velocities and,

consequently, neither have they found that the former is underestimated with respect to the latter. The findings from the current studies therefore have important implications for Johansson's models of "vector analysis" and biological motion, to which they lend considerable empirical support. The results lend equal support to the differential processing account of induced motion as first proposed by Duncker (1929/1955), who attributed the illusion to the underestimation of the NOR component velocity.

The first three studies have shown that the three separate spatial context-determined velocity misperceptions explored in this thesis, induced motion, the DI and the SDI, display characteristics that are consistent with the proposed differential processing account of velocity perception. That these three illusions appear to arise from this single mechanism is an important finding, which in turn has important implications for the spatial context-determined visual perception of motion. The three illusions manifested respectively from three diverse stimulus configurations, a point emphasised by the efficacy of a static inducer in producing the SDI. Yet, apparently because all three stimuli contained veridical velocities comprising both NOR and OR components, differential processing could account for all three illusions. It is therefore not unreasonable to infer that other instances of velocity misperception encountered in stimuli comprising both NOR and OR components – see Anstis and Casco's (2006) 'flying bluebottle illusion' and Dürsteler's (2006) 'freezing rotation illusion' for compelling examples – are likely to be attributable to the same mechanism. More generally, consideration should be given to the fact that almost all commonly observable motions are composed of both NOR and OR components, and will therefore be shifted perceptually from their veridical trajectories due to the effects of differential processing.

While only one of the current studies was specifically concerned with identifying the neural locus of the DI and thereby potentially of differential processing, all of the current studies

have produced results that hold implications for the neurophysiological mechanisms involved. If the DI arises from the differential processing of NOR and OR component velocities, as the current findings suggest, drawing on existing evidence from research on relative motion should provide insights into the DI's neural underpinnings. For example, relative motion studies could provide clues as to the direction illusion's neural locus (or loci). As outlined in the introduction, neurophysiological studies have identified the neural mechanisms purportedly responsible for extracting both NOR and OR velocities within each of the three main processing stages of the visual motion pathway (e.g. Born & Tootell, 1992; Davidson & Bender, 1991; Eifuku & Wurtz, 1998; Jones et al., 2001; Orban, Gulyas & Spileers, 1987). However, if OR component velocities are extracted via CRF-surround activity, as is purportedly the case, and if the DI arises from differential processing, as is suggested by the current study, the spatial scale of the CRFs must be sufficiently small to extract the local direction imbalances present in a bidirectional RDK. As discussed in the introduction, only the V1 CRF-surround mechanism is of a suitable scale to detect the local velocity discontinuities. Concordantly, psychophysical studies indicate the possible early extraction of OR component motion and later extraction of the NOR component (e.g. Symons et al., 1996). If this is the case, the implication that the DI is therefore likely to arise from multilevel activity may help to explain the discrepancies in the literature regarding the DI's neural substrate. Conversely, empirical findings from studies of the DI and induced motion may help us to better understand the mechanisms involved in differential processing. For example, the sizes of both induced motion and the DI are reduced considerably (by between 60 and 80%) when the test and inducing stimuli are presented to different eyes, i.e. dichoptically (Day & Dickinson, 1977; Grunewald, 2004; Marshak & Sekuler, 1979; Wiese & Wenderoth, 2007; 2010). Because MT cells are exclusively binocular and therefore respond to stimulation in either eye (Maunsell & van Essen, 1983) while many V1 cells respond only to monocular input

(Merigan & Maunsell, 1993; Poggio & Poggio, 1984), the attenuation of both induced motion and the DI during dichoptic viewing suggests that at least some of the processing responsible for the illusions occurs in V1.

Attributing the DI to differential processing also holds other important implications for the mechanisms involved in the extraction of component velocities. Our perception of an object's velocity is usually attributed to activity in neuronal populations that respond to specific veridical directions of motion. Direction selectivity is a distinguishing characteristic of area MT, which contains a preponderance of such cells (Albright, 1984; Albright & Stoner, 1995; Zeki, 1974), and activity changes in MT have been found to correlate well with perceptual changes (Britten et al., 1992; Castelo-Branco, Formisano, Backes, Zanella, Neuenschwander, Singer & Goebel, 2002; Qian & Andersen, 1994; Salzman, Britten & Newsome, 1990; Van Wezel & Britten, 2002). However, if we accept the contentions of the differential processing model, from the misperceptions of velocity presented here and elsewhere it is evident that the perceived velocity of an object is determined not by its veridical velocity but by its NOR and OR component velocities within its larger spatial context. Further, each of these components can differ from the veridical (and perceived) direction by up to 90° and, particularly in the case of the NOR component velocity, from the veridical (and perceived) speed. The current findings therefore suggest the involvement of neural responses to component directions and speeds rather than the veridical (and perceived) velocity. The involvement of early (V1) processing in OR motion perception has been suggested previously (e.g. Baker & Graf, 2010; Paffen et al., 2004) and is supported by neurophysiological findings showing that many V1 cells respond better to OR motion than they do to NOR motion (Bridgeman, 1972; Cao & Schiller, 2003; Hupe, James, Payne, Lomber, Girard & Bullier, 1998; Kleinschmidt, Thilo, Buchel, Gresty, Bronstein & Frackowiak, 2002; Reppas, Niyogi, Dale, Sereno & Tootell, 1997). A much smaller proportion of

V1 cells than MT cells are tuned to a specific direction (Albright, 1984; Albright & Stoner, 1995; De Valois et al., 1982; Hawken et al., 1988; Mikami et al., 1986; Zeki, 1974), while many are likely to code opposing (180°) motions irrespective of the absolute veridical orientation of their trajectories (Dellen et al., 2005; Shen, Xu & Li, 2007). Such characteristics are ideal for extracting OR motion signals (Joly & Bender, 1997) since the OR direction of an object is determined by its spatial relationship to other objects in the visual field irrespective of the object's veridical direction, from which the OR direction is likely to differ greatly, as demonstrated in the current thesis.

6.3 Considerations for a future model

6.3.1 Assimilation effects

The conventional DI has been found to switch from a repulsive shift in perceived direction, i.e. a directional shift away from the inducing direction, to one of attraction at small direction separations, with the transparent bidirectional motion percept becoming one of coherent unidirectional motion (Braddick et al., 2002; Mather & Moulden, 1980). Consideration needs to be given to how the differential processing model might accommodate the occurrence of such assimilation effects. One possible explanation may lie in the spatial threshold of OR motion perception, as was discussed above. At small direction separations, the OR component velocity and displacement is at a minimum. If the dot density in the bidirectional RDK is high enough that a sufficient number of dot pairs moving apart in OR motion fall within a V1 CRF, the OR component velocity will not be detected. Concordant with this notion, Braddick, Wishart, and Curran (2002) found that increasing the density of an already dense bidirectional RDK resulted in a reduced DI. Dakin and Mareschal (2000) found that increasing inducer density increased DI in the test, but this result is more likely due to a directional shift in the NOR component, since the display was thus no longer symmetrical. Assimilation has been shown to persist for much larger

direction separations (30°) when the bidirectional RDK component contrast is reduced to perithreshold levels (Levinson et al., 1980). This could possibly reflect the fact that the V1 neuron's optimal stimulus size is larger at low than at high contrast (Cavanaugh et al., 2002; Ichida, Schwabe, Bressloff & Angelucci, 2007; Kapadia, Westheimer & Gilbert, 1999; Levitt & Lund, 1997; Sceniak, Ringach, Hawken & Shapley, 1999). Two studies of direction shifts using static inducers report similar assimilation effects (Anstis, 2012; Masson, Dodd & Enns, 2009). Masson, Dodd and Enns (2009) found that a dot moving horizontally along the zero-crossing of a sinusoid defined by a pair of 'rails' would appear to oscillate vertically. They found that when the dot had a diameter of 0.15° and the rails were separated by 0.5° , the oscillation was 90° out of phase with the sinusoid, indicating that the dot's trajectory was being shifted away from the local segments of the rails. However, when the dot diameter was reduced to 0.075° and the rail separation to 0.054° , the oscillation was in phase with the sinusoid, indicating assimilation. These findings again show that assimilation occurs at a scale that corresponds to the size of V1 CRFs. The size of V1 receptive fields increases linearly with eccentricity (see Murakami & Shimojo, 1996). It might therefore be expected that assimilation effects would be more prevalent with peripheral viewing and, moreover, that they would correspond with eccentricity in a linear relationship. This is precisely what occurs with the 'furrow' illusion (Anstis, 2012), in which an object's motion trajectory is perceptually shifted toward the orientation of a stationary grating. Using a grating oriented 45° from vertical, Anstis (2012) found that the illusion was absent during foveal viewing, contrary to other findings including our own, but that it increased linearly with eccentricity until, at an eccentricity of 24 degrees, it reached its maximum 45° shift, with the motion trajectory perceived to be parallel to the grating.

A second possible explanation for the assimilation effect is that at very small angles the OR component velocity is so small that it lies near or below detection threshold. Murakami

(2004), using two concentric stimuli with a translating central RDK surrounded by an annulus of static noise, measured the velocity detection threshold of OR motion to be ~ 0.04 deg/s. The stimulus duration was 0.85 s. Braddick et al (2002) observed attraction in a bidirectional RDK with each set of dots drifting at 5 deg/s with a direction separation of 22.5° , and Mather and Moulden (1980) found that subjects perceived unidirectional motion in a bidirectional RDK when direction separations were less than $\sim 15^\circ$. In the Braddick study, the OR component velocity of each set of dots was 0.975 deg/s, substantially higher than the threshold found by Murakami. However, Braddick et al. (2002) used a stimulus in which the lifetime of each dot was only 0.1 s. It has been shown that reducing the stimulus duration elevates velocity detection thresholds considerably (Shioiri et al., 2002). It is therefore very likely that observers' ability to detect the OR component velocity in the Braddick study was compromised. Mather and Moulden (1980) used dot speeds of 2.34 (test) and 2.58 deg/s (inducer). The OR component velocity of each set was therefore ~ 0.3 deg/s, which was likely to have been peri-threshold since each dot had a lifetime of only 0.288 s. Quite possibly, then, attraction effects and the failure to detect two directions of motion in a bidirectional RDK are due to observers' compromised ability to detect the OR component velocity.

6.3.2 Speed dependency of the SDI and DI

In Chapter 4, we noted that the SDI is unlikely to result from an induced shift in perceived vertical due to the presence of the line. Further evidence that this is not the case can be inferred from the third experiment in Chapter 3, where it was shown that the size of the SDI is speed-dependent. If the SDI were the result of a shift in perceived vertical, such speed dependency should not be observed. Having found a significant inverse relationship between dot speed and SDI magnitude, and since the same effect has been reported to occur in the conventional DI (Braddick et al., 2002; Rauber & Treue, 1999), we are faced with the question of how such an

effect might be attributed to the differential processing model. By decreasing the veridical velocity from 8 deg/s in the SDI fast condition to 0.5 deg/s in the SDI slow condition, we were thereby also decreasing both the OR and NOR component velocities. Since we know that the visual system has a greater sensitivity to OR than of NOR motion, there is a strong possibility that reducing the OR and NOR component velocities equally does not affect their respective perceived velocities equally. There is some evidence for such an asymmetrical relationship. Smeets and Brenner (1994), for example, found that reaction times to OR and NOR motion were approximately equal for stimulus velocities $> \sim 8$ deg/s, but that with decreasing velocities reaction times for NOR motion increased exponentially with respect to those for OR motion.

The occurrence of assimilation and the speed effects reported in DI studies are therefore not necessarily in conflict with the differential processing model. Rather, they stand to provide insights into the mechanisms involved in OR motion processing, and may therefore guide future improvements of the differential processing model, which will need to take such effects into consideration.

6.3.3 What constitutes the NOR component velocity?

One question that a definitive model of differential processing must ultimately address is that of what constitutes the NOR component velocity. Unlike Johansson, who defined the NOR component velocity as the ‘common’ motion in the display, Dakin and Mareschal (2000) suggested that the NOR component velocity in a bidirectional RDK is more likely to be equivalent to the vector average of the local velocities in the display. When the two sets of dots are symmetrical, i.e. are of equal density, contrast and speed, both the vector average and the common component will fall at an angle midway between the two drift directions and will be of equal magnitude. However, when considering asymmetrical stimuli, evidence from several studies indicates that a vector average calculation provides a more tenable estimate (e.g. Dakin &

Mareschal, 2000; Proffitt et al., 1979; Royden & Connors, 2010). Defining the NOR component as the vector average finds agreement with the studies outlined in Section 1.5.4, which suggest that local velocities are integrated as the vector average, and it further provides for the occurrence of induced motion. Induced motion can be observed when the test and inducing stimuli are each a single dot (Day, Millar & Dickinson, 1979; Duncker, 1929/1955; Mack et al., 1975). Figure 4 illustrates how induced motion in one dot due to the motion of a second dot can be explained in terms of differential processing when the NOR component velocity is represented by the vector average of all velocities in the display. Dot A has a veridical velocity of 0 deg/s. Dot B has a veridical velocity of 2 deg/s rightward, so from T1 to T2, it has moved 2 deg rightward. The OR component motion, the motion of Dot B relative to Dot A is 2 deg/s. The NOR component velocity is denoted by the displacement of the 'x', being 1 deg rightward from T1 to T2. Since differential processing posits that the NOR component is perceptually underestimated with respect to the OR component, as depicted in T2P (T2 perceived), Dot A is perceived as moving leftward. Note that since there is no motion that is common to both dots, such a representation of the NOR component velocity does not explain the motion induced in the left dot. IM studies have found that when a stationary stimulus is induced to move, the speed of the inducing stimulus is underestimated (Rock et al., 1980). Correspondingly, in the diagram the rightward velocity of Dot B is perceptually underestimated. Note that it is not necessarily the case that the OR component is perceived veridically, but only that the OR component velocity is underestimated to a lesser degree than the NOR component velocity, as was demonstrated in Chapter 4.

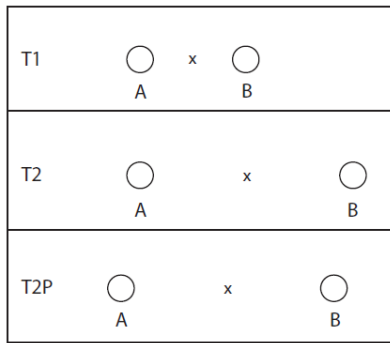


Figure 4. Diagram illustrating how induced motion results from the underestimation of the NOR component velocity, defined as the vector average of all motions in the display. Veridical velocities of Dots A and B are represented by their respective displacements from T1 to T2, and the NOR component velocity, which is the vector average, is represented by the displacement of x from T1 to T2. The perceived velocities of Dots A and B and their vector average are represented by their respective displacements from T1 to T2P. Because of the underestimation of the NOR component velocity, the velocity of Dot B is also underestimated and Dot A is seen to move leftward. Note that the OR component, being the difference between A and B, is perceived veridically in this case.

6.4 Conclusion

Differential processing has here been proposed as a potential mechanism underlying a variety of spatial context-related visual motion phenomena. The proposed account contends that veridical velocities are decomposed into two perceptually distinct component velocities, one object-relative and the other non-object-relative, and that the latter is underestimated with respect to the former by a constant proportion. The research presented here has investigated whether a hypothesis based on differential processing constitutes a credible proposition by determining whether it can potentially explain various instances in which the velocity of an object is misperceived. The studies comprising this thesis have explored characteristics of induced motion, the direction illusion and the new statically induced direction illusion to test the tenability of ascribing these diverse phenomena to the same single underlying mechanism. The studies have shown that these phenomena display characteristics consistent with the occurrence of differential processing, and it is concluded that such a mechanism is likely to affect our perception of velocities in our day-to-day existence. An attempt to define a more formal differential processing

model proved highly successful in predicting the general pattern of results, particularly the quantitative measurements of perceived direction. It was, however, less than ideal as a predictor of perceived speed. Possibly, with some further development, the formalised model will be able to account for the quantitative data from a diverse range of visual motion illusions.

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Appendix A

Manuscripts 1, 2 and 4 in published format

Studies of the angular function of a Duncker-type induced motion illusion

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Abstract. Duncker (1929/1955, *Source Book of Gestalt Psychology*, pp 161–172) demonstrated a laboratory version of induced motion. He showed that, when a stationary spot of light in a dark laboratory is enclosed in an oscillating rectangular frame, the frame is perceived as stationary and the dot appears to move in the direction opposite the true motion of the frame. Zivotofsky (2004, *Investigative Ophthalmology & Visual Science* **45** 2867–2872) studied a more complex variant of the Duncker illusion, in which both the inducing and the test stimuli moved: a single red test dot moved horizontally left or right while a dense background set of black dots on a white background moved vertically up or down. When the background inducing dots moved up (down), the truly horizontally translating test dot appeared to drift at an angle down (up) from the horizontal. In experiment 1, we used two methods to measure the complete angular function of the Zivotofsky effect and found it to peak with an inducer–test direction separation of approximately 30°, similar to the inducing angle that has been found to maximise other direction illusions. Experiment 2 tested and confirmed predictions regarding the effects of relative test and inducer speeds based on the vectorial subtraction of the inducing velocity from the test velocity.

Keywords: induced motion, relative motion, direction illusion

1 Introduction

A common occurrence of illusory induced motion (IM) occurs when the moon is seen through drifting clouds: the illusory percept is that the clouds are stationary and the moon is drifting in the direction opposite to the true cloud movement. Wade and Swanston (1987, page 555) quoted Porterfield (1759) as an early observer of this phenomenon:

“If two or more Objects move with the same Velocity, and a third remain at rest, the Moveables will appear fixed, and the Quiescent in Motion the contrary Way. Thus, Clouds moving very swiftly, their Parts seem to preserve their Situation, and the Moon to move the contrary Way.”

Reinhardt-Rutland (1988) published a comprehensive review of research on IM.

Duncker (1929/1955) first demonstrated a laboratory version of IM. He showed that a stationary spot or point of light surrounded by a luminous moving frame will appear to move in a direction opposite to that of the physical motion of the frame. In addition, if the frame’s motion is below the subject-relative motion detection threshold, the frame also appears stationary. In order to produce IM, it is not necessary that the inducing object surrounds the test object. For example, induced motion can also be demonstrated when the test and inducing objects both are spots of light (Day et al 1979; Duncker 1929/1955; Mack et al 1975). In this case either or both spots may appear to move even though only one spot is actually moving.

Zivotofsky (2004) studied what he called a more complex variant of the Duncker illusion, in which both the inducing and the test stimuli moved: a single red test dot moved horizontally left or right while a dense background set of black dots on a white background (50% density) moved vertically up or down. The illusion was such that when the background inducing dots moved up (down), the truly horizontally translating test dot appeared to drift at an angle down (up) from the horizontal. There were large individual differences between the

seven observers, but the illusions obtained were often extremely large, ranging from about 5° to greater than 80° , with several observers exhibiting illusions close to 40° and an overall mean illusion across all conditions of about 26° . In a control condition when the background inducing dots were stationary, illusory errors were negligible, averaging 2.3° .

Zivotofsky's stimuli were presented on a $20^\circ \times 20^\circ$ area of a back-projection screen, and he suggested that the large illusions he obtained were due to the observers' tendency to attribute the background motion to eye movements pursuing the target, just as in the real world, when a moving target is pursued, the motion of the background on the retina is not attributed to movement of the background itself. Zivotofsky's findings confirmed earlier results to which he did not refer (Gogel 1979).

Gogel (1979) showed that the real motion of a target dot (say, vertical) and IM induced by a drifting background (say, horizontal) sum. Thus, the phenomenal target trajectory is a vector sum of its physical motion and illusory IM induced by the drifting background. The target's perceived direction of motion is diagonal. Figure 1, adapted from Gogel (1979), illustrates this. In figure 1, a spot (s) moves vertically (v) but is enclosed in a frame moving left. The frame induces horizontal rightward motion (h) in the spot. The resulting vector sum percept of v and h is m.

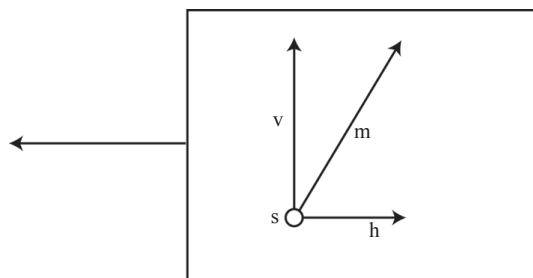


Figure 1. Adapted from Gogel (1979, *Perception* 8 255–262). Here, a spot (s) moves vertically (v) but is enclosed in a frame moving left. The frame induces horizontal motion (h) in the spot. The resulting vector sum percept of v and h is m.

There is, however, one critical difference between the methods of measurement of the perceived spot path used by Gogel and by Zivotofsky. Gogel had observers set two posts to indicate the apparent horizontal distance (h) moved by the truly vertically moving spot (v) that had no physical horizontal component at all. He had them rotate a rod to indicate the apparent direction of motion of the spot. Zivotofsky used a staircase procedure (eg Wetherill and Levitt 1965) to null the illusory diagonal trajectory of the target. That is, the physical direction of the target was altered until the observer perceived the target to be moving horizontally. Such a nulling method was also used to measure IM by Levi and Schor (1984).

Because the illusory effects are very large with the Zivotofsky-type display, there is a fundamental flaw in Zivotofsky's methodology. When nulling methods are used with small tilt aftereffects (say, 2°), it may not much matter that a fixed inducer at, say, 15° is actually only $15^\circ - 2^\circ = 13^\circ$ away from the test when the aftereffect has been nulled, but with very large effects it matters a lot. For example, in the case of Zivotofsky's observer who had an illusory direction shift of more than 80° , when the illusion was nulled, the actual angle between the target and inducing direction would no longer have been 90° but less than 10° , ie 90° minus 80° or more.

Zivotofsky used only orthogonal inducing and test stimuli. We wished to measure the complete angular function of illusions induced by a Zivotofsky-type display—that is, the magnitude of the illusory direction shift as a function of the angular separation of inducing

and test directions. Studies of direction repulsion illusions have commonly used transparent motion stimuli (superimposed random dot kinematograms, or RDKs) with the finding that the perceived direction of the test RDK (arbitrarily defined as one of the two superimposed RDKs) is shifted between 10° and 20° away from the inducing direction (arbitrarily defined as the other RDK) and that the angular function shows a peak effect between about 20° and 40° inducer–test direction separation (Marshak and Sekuler 1979; Rauber and Treue 1999; Wiese and Wenderoth 2007). It would be consistent with the hypothesis that the IM display used by Zivotofsky belongs to the same class of direction repulsion illusions as these if the Zivotofsky effect also exhibited peak effects at 20° to 40° angular separation between test target direction and inducer direction. Establishing the angular separation between test and inducer directions at which the peak effect occurs was the first aim of experiment 1.

The second aim of experiment 1 was to measure the angular function of the direction shift in two ways with staircases. First, we repeated Zivotofsky's nulling method with the motion direction of the inducer fixed so that the test–inducer direction difference varied depending on the magnitude of the direction shift. Second, we yoked the inducer direction to the test direction so that the test–inducer angle remained constant. It was predicted that the two angular functions would peak at different nominal test–inducer angles. It was also predicted that, if the first function were replotted with the true inducing angle (nominal angle minus illusory direction shift), it would coincide with the second function.

2 Experiment 1

2.1 Method

2.1.1 *Apparatus.* VPixx v2.3 software (VPixx Technologies Inc, Longueuil, Canada, <http://www.vpixx.com>) generated all stimuli and recorded all responses in an Excel file on a G5 Macintosh Dual 2 GHz Power PC running Mac OS X version 10.4.11. The SONY Trinitron Multiscan G520 monitor had a frame refresh rate of 75 Hz and a pixel resolution of 1152 × 870. Subjects viewed the screen binocularly from a distance of 57 cm through a circular viewing tube (length 57 cm, diameter 33 cm) that was lined internally with matte black felt and that masked the edges of the monitor. A chinstrap and headrest prevented head movement. Left and right arrow keys on a standard Apple keyboard were used to indicate that the red dot was perceived to be drifting left or right of vertical.

2.1.2 *Subjects.* There were fifteen subjects from an introductory psychology course who volunteered in return for modest course credit. All were emmetropic or wore their usual corrective lenses.

2.1.3 *Stimuli.* A random pattern of 0.18 deg of visual angle white inducing dots (1 dot deg⁻²) on a black background drifted at a speed of 3 deg s⁻¹ at angles of 0° (vertical), ±7.5°, ±15°, ±22.5°, ±30°, ±37.5°, 45°, ±60°, ±90°, or ±120°. Michelson contrast, defined as $[L_{\max} - L_{\min}] / [L_{\max} + L_{\min}]^{-1}$ was 0.98. In all of these inducing conditions, a 0.6 deg red test dot, when drifting physically vertical, drifted at 3 deg s⁻¹ from 5 deg below the centre of the screen to the top screen centre. As the test trajectory changed, the starting position of the dot followed an arc with a radius of 5 deg from the screen's centre so that it always passed through the centre of the screen. The circular viewing tube masked the display edges to remove all cues to true vertical and horizontal. The circular inducing dot field subtended 33 deg. Stimuli were presented for a maximum of 1 s, but subjects were instructed to respond as soon as they felt able to make a decision as to whether the red dot appeared to be drifting left or right of vertical. If no response had been registered before stimulus offset, a grey background was presented until a response was registered.

There were two reasons for using a short 1 s presentation. First, the task was very easy so that 1 s was ample time to make the judgment. Second, subjects were specifically instructed to respond to the initial perceived direction of motion of the test dot because the authors had observed that its path often appeared to curve with long exposure durations. This curvature was towards true vertical, the opposite of that which was reported previously (Post and Chaderjian 1988). In our case we think this occurred because as the dot nears the top of the aperture with a long exposure there are increasingly obvious cues to the fact that the dot is still in the centre of the screen, with positional cues thus countering the illusory shift in the direction away from true vertical.

There was no fixation point and free inspection was permitted because Zivotofsky (2004) found that when he used presentation times of 200 ms and 50 ms, four of his six observers obtained non-significantly different effects at the two exposure durations and two obtained significantly larger effects at the shorter duration that was too brief for target tracking to occur. Zivotofsky (2004) concluded: “Our data with the 50-ms exposure rule out any role of eye movements in generating the illusion” (page 2870).

2.1.4 Procedure. For each inducing angle, a single staircase procedure was used to measure the point of subjective vertical motion of the test dot. Whenever the observer pressed the left arrow key to indicate perceived test stimulus motion left of vertical, the staircase procedure moved the test trajectory to the right, and vice versa. Pilot studies indicated that most direction shifts were so large that it was adequate to begin each staircase with the red dot moving in the true vertical direction. Step sizes for each reversal were 10°, 5°, 4°, 3°, 2°, and 1° thereafter. Each condition was terminated after 10 reversals, with the mean of the final 8 reversals from each staircase averaged to give the estimated point of subjective vertical motion (PSVM).

Measurements were counterbalanced with an equal number of trials conducted with a clockwise (CW) oriented inducing display and a counterclockwise (CCW) oriented inducing display. Because there were so many inducing angles, the one-hour testing session was divided into 6 blocks of staircases with a 2-minute break between blocks. The 6 blocks were as follows. Blocks 1–3 used inducing angles that were fixed (as Zivotofsky had done) so that a nominal inducing angle of θ° was truly θ° only when the test dot was actually drifting vertically. Otherwise, the actual inducing angle was the nominal fixed angle minus the illusory direction shift. Blocks 4–6 had test-relative inducing angles so that the inducer was at a variable absolute angle that always kept the angle between the test and inducing direction at θ° . For example, in Blocks 1–3, when the inducing angle was horizontal right (90°) and the test angle was vertical (0°), the inducing minus test angle was $90^\circ - 0^\circ = 90^\circ$. But if the staircase procedure changed the test angle to, say, 60°, then the inducing minus test angle reduced to only $90^\circ - 60^\circ = 30^\circ$ because the inducing angle was fixed at 90°. In Blocks 4–6, however, if the test angle became 60°, the inducing angle changed from 90° to $90^\circ + 60^\circ = 150^\circ$ so that the inducing minus test angle was always maintained at 90°.

Each subject completed the 6 blocks in a different random order. Inducing angles were: in Blocks 1 and 4, $\pm 0^\circ$, $\pm 15^\circ$, $\pm 45^\circ$, and $\pm 90^\circ$; in Blocks 2 and 5, $\pm 7.5^\circ$, $\pm 22.5^\circ$, and $\pm 37.5^\circ$; and in Blocks 3 and 6, $\pm 30^\circ$, $\pm 60^\circ$, and $\pm 120^\circ$. Within each block, the 6 (Blocks 2, 3, 5, and 6) or 8 (Blocks 1 and 4) inducing orientations were randomly interleaved.

Prior to the start of the experiment, subjects were given brief practice trials with fixed inducing angles only of $\pm 0^\circ$, $\pm 45^\circ$, and $\pm 90^\circ$ ($\pm 0^\circ$ simply means that this condition was repeated). As in the experiment to follow, the 6 practice staircases were randomly interleaved and terminated after 6 reversals.

2.2 Results

PSVMs for CW and CCW inducing trials were combined and reported as single values measured in degrees CCW of vertical, as if all conditions incorporated an inducing direction CW of the test direction. Since CW and CCW measurements were counterbalanced, no baseline adjustments (pretests) were necessary. The means and standard errors of the illusory direction shifts obtained are shown in figure 2.

Two examples of the data shown in figure 2 can be used to explicate the data plotted as “actual fixed inducer”. For a fixed inducer of 90° , the direction shift is 60.07° . This means that the red dot appeared to move vertically when actually moving 60.07° CW. Because the fixed inducer was still drifting horizontally at 90° , the true angle between the test and inducing directions was $90^\circ - 60.07^\circ = 29.93^\circ$. Hence, in the actual fixed inducer data the illusion of 60.07° is plotted above 29.93° on the abscissa. In the case of the fixed 30° inducer the direction shift was 25.15° . This means that the actual angle between the test and inducer directions when the test appeared to drift vertically was $30^\circ - 25.15^\circ = 4.85^\circ$. So, in the actual fixed inducer data the direction shift of 25.15° is replotted above the direction 4.85° on the abscissa.

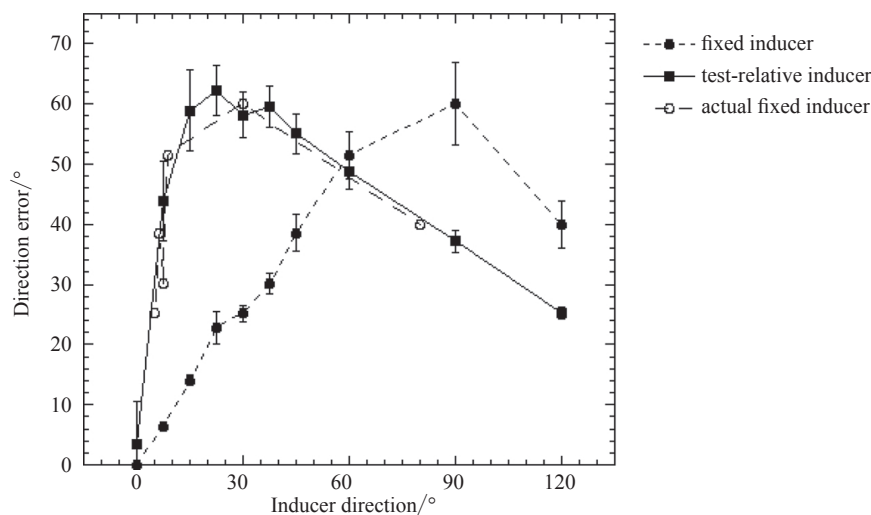


Figure 2. Means and standard errors of PSVMs (illusory direction shifts). Inducing direction 0° = vertical, 90° = horizontal. Fixed inducer refers to conditions in which the inducing direction was always the direction shown on the abscissa, regardless of the motion direction of the test dot. Test-relative inducer refers to conditions in which the inducing direction varied with the direction of the test dot to keep the angle between test direction and inducing direction constant and equal to that shown on the abscissa. Actual fixed inducer plots the fixed inducer illusions but at the real inducing angle—namely, nominal inducing angle shown on the abscissa minus the PSVM or illusory direction shift.

2.3 Discussion

Experiment 1 was designed to measure the complete angular function of the illusory direction shift in two ways with staircases. First, we repeated Zivotofsky’s (2004) nulling method with the motion direction of the inducer fixed so that the test–inducer direction difference varied depending on the magnitude of the direction shift. Second, we yoked the inducer direction to the test direction so that the test–inducer angle remained constant regardless of the test dot’s direction. It was predicted that the two functions would peak at different nominal test–inducer angles but that if the first function were replotted with the true inducing angle (ie nominal inducing direction minus direction shift magnitude), it then would coincide with the second function. Clearly, figure 2 very strongly supports that reasoning and, in our view, validates the method of yoking the inducing motion direction to the direction of the test dot.

In the introduction, we noted that if the IM display used by Zivotofsky belongs to the same class of direction repulsion illusions reported by Marshak and Sekuler (1979), Rauber and Treue (1999), and Wiese and Wenderoth (2007), then it too might be expected to exhibit peak effects at 20° to 40° angular separations between test target and inducer direction separations (see the last two paragraphs of the introduction).

Figure 2 shows that in the fixed inducer condition the illusory direction shift appears to exhibit a peak effect at a test–inducer motion direction difference of 90°. However, when this angular function is replotted with the real fixed inducer calculation, it exhibits a peak illusion of 60.07° at 29.93°, very close to 30.00°. Consistent with this, the angular function of the illusion in the test-relative inducer condition peaks between 15° and 37.5° test–inducer direction difference with illusions at 15.0°, 22.5°, 30.0°, and 37.5°, respectively, of 58.9°, 62.3°, 58.1°, and 59.6°.

3 Towards a model of IM

As we have seen, Gogel's (1979) model is based on the principle that IM and physical motion can be vectorially summed. If this is true, then, as depicted in figure 3, IM must result from a perceptual change in the speed of the motion component that is parallel to the inducer (x), while the motion component that is orthogonal to the inducer (y) will remain unchanged.

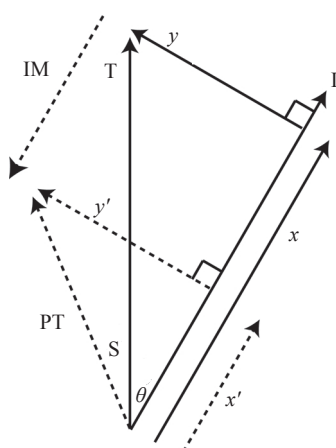


Figure 3. Vector diagram used to calculate the magnitude of induced motion (IM). Actual motion vectors are represented by solid arrows and perceptual vectors by dashed arrows. The test velocity (T) is vertical. θ is the directional separation of test and inducer, so the inducing velocity (I) has a direction θ° CW of vertical. S is the shift in the perceived direction of the test, so the perceived test velocity (PT) has a direction S° CCW of vertical. The test velocity is broken down into two component velocities, that which is parallel to the inducer (the x component) and that which is orthogonal to the inducer (the y component). The perceived test velocity is also broken down into parallel (x') and orthogonal (y') components. The IM is opposite the inducing direction and can be calculated as the difference between x and x' .

In experiment 1, our independent variable was the test–inducer direction difference, θ , and the speed of both test (T) and inducer (I) was fixed at 3 deg s^{-1} . In addition, the component velocities, x and y , were known quantities: $y = 3 \cdot \sin(\theta)$ and $x = 3 \cdot \cos(\theta)$. For each value of θ , we obtained a value for our dependent variable, the shift in perceived direction, S . To obtain a measurement of IM, we first calculated the value of the perceptual speed of the x component (x') and subtracted this from its actual speed (x). We found the mean IM value across test–inducer differences (θ) to range from 2.272 deg s^{-1} when $\theta = 120^\circ$ to 2.650 deg s^{-1} when $\theta = 22.5^\circ$. A set of one-sample two-tailed t -tests found the effect to be significantly different from zero for all measured inducer directions ($t_{14} \geq 15.559$, $p < 0.0005$, $\eta^2 = 0.945$). A one-way repeated measures ANOVA found the main effect of direction difference to be small but significant ($F_{8,112} = 3.402$, $p = 0.002$). Pairwise comparisons found significant differences between the $\theta = 22.5^\circ$ and $\theta = 90^\circ$ conditions ($p = 0.020$), between the $\theta = 37.5^\circ$ and $\theta = 90^\circ$ conditions ($p = 0.012$), and between the $\theta = 37.5^\circ$ and $\theta = 120^\circ$ conditions ($p = 0.044$) only (p -values were Bonferroni-adjusted to control for overall error rate). Although the main effect of direction difference was significant, because it was so small, we considered ourselves justified in calculating the IM averaged across direction differences (IM = 2.488 deg s^{-1} ; SE = 0.105).

If the perceived test direction (PT) results from a vector sum of IM and the actual test direction (T), we should be able to predict, to a very close approximation, the results of experiment 1 with our single obtained value of IM. These predictions are presented in the graph in figure 4, which shows predicted values that very closely resemble the data obtained in experiment 1 (yoked inducer data replotted from figure 2). The results obtained in experiment 1 can therefore be summarised almost entirely by the vectorial model $PT = T - IM$.

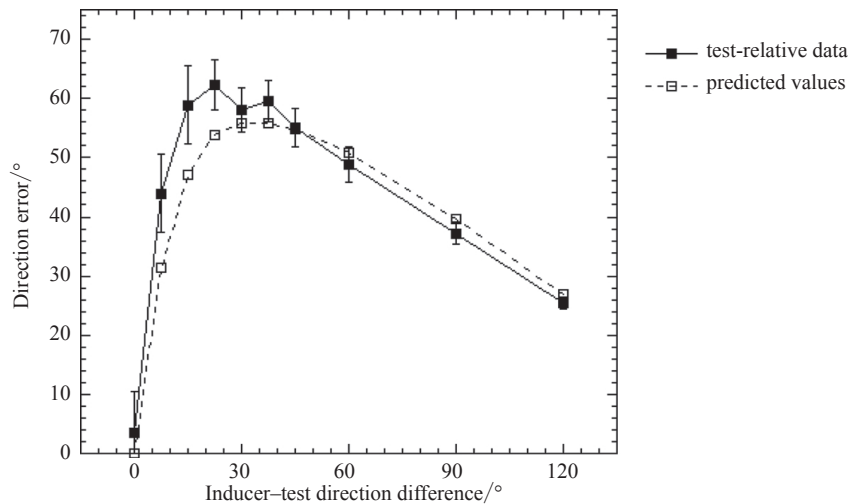


Figure 4. The shift in perceived test direction across inducer–test direction differences as obtained in experiment 1 with the yoked inducing direction (solid plot) and as predicted by the model $PT = T - IM$ (dashed plot). Shifts were calculated from a single IM value of 2.488 deg s^{-1} .

4 Experiment 2

The aims of this experiment were: (i) to test several predictions made by Gogel’s (1979) model regarding the effects of the relative speeds of the inducing dots and the test dot on the illusory direction shift, through the use of the yoked staircase method; and (ii) to establish a simple vector-subtraction model of the direction shift that can account for the effects of varying inducing and test speeds.

Two of our predictions can be derived from figure 5. In comparison to (a) and (b), the faster inducing speed in (a) results in a larger direction shift because the perceived trajectory of the test dot in (a) is further from the true vertical direction than it is in (b). That is: $(90^\circ - \alpha) > (90^\circ - \beta)$. So, the first prediction was that systematically increasing inducing speed would systematically increase the magnitude of the illusory direction shift. Zivotofsky (2004) reported some relevant evidence, but he did not vary inducing speed systematically. Rather, he ran one condition in which test and inducer speeds were both 20 deg s^{-1} and another in which inducer speed remained at 20 deg s^{-1} , but test speed was increased to 40 deg s^{-1} . He reported (page 2870) that the illusion was 56% weaker in the latter condition. Figure 5c shows that when the ratio between the test and inducing speeds is held constant, in this example 1.37:1, the angle (λ) between true vertical and PT—the illusory direction shift—should be constant. This was the second prediction tested in experiment 2. When we later present the results of experiment 2, it will be seen that there are no data points for inducer speeds of 6.25 deg s^{-1} and 7.5 deg s^{-1} at inducer–test direction differences of 30° and 60° . The reason can be explained with figure 5d. When the test-to-inducer speed ratio is very small and the inducer–test direction separation is small, the test dot is perceived to be drifting down. Because pilot subjects found this confusing, we decided not to run those conditions.

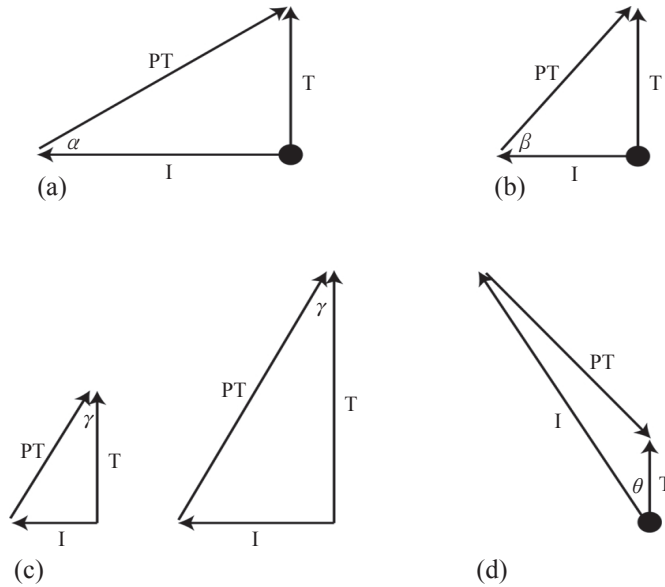


Figure 5. In all vector diagrams T is the true test dot direction and speed, I is the inducing direction and speed, and PT is the perceived test dot trajectory.

A third prediction can be derived from figure 3. The two methods of measuring IM described in experiment 1, one with a fixed inducer and the other with a yoked inducer, produced respective peaks in direction shift (S) at $\theta = 90^\circ$ and $\theta = \sim 30^\circ$. In the former case, the results are reported as a function of the perceived angular separation ($\theta + S$) of test and inducer. In fact, such results must show a peak at $\theta + S = 90^\circ$ because it is geometrically determined. Consider the trigonometric identity: $IM \sin(S)^{-1} = T \sin(\theta + S)^{-1}$. From this identity, we can formulate the following equation (see figure 3):

$$S = \sin^{-1} [IM T^{-1} \cdot \sin(\theta + S)] . \quad (1)$$

From equation (1), we can state that for any given constant IM value, the closer to 90° the perceived directional difference between inducer and test ($\theta + S$), the larger the directional shift (S) will be. The greatest shift (S) must therefore occur when $\theta + S = 90^\circ$. We have also observed, using the yoked inducer method, that S peaks when $\theta = \sim 30^\circ$ (actually between 22.5° and 45.0°). It can be seen from figure 3 and from equation 1 that the greater the IM, the greater S will be. So, if we can increase the IM, we will also increase S. And since S is greatest when $\theta + S = 90^\circ$, S will peak at a smaller value of θ . From experiment 1, IM was calculated to be $\sim 2.5 \text{ deg s}^{-1}$, and S was found to peak at $\theta = \sim 30^\circ$. Therefore, if $IM > 2.5 \text{ deg s}^{-1}$, S should peak at $< 30^\circ$, and with increasing IM, S will peak at decreasing values of θ . Since we have predicted that IM will increase with inducer speed, S should peak at decreasing values of θ as inducer speed is increased. This was a further prediction that we wished to test in experiment 2.

4.1 Method

Most aspects of methods were as in experiment 1. Differences were as follows. There were 120 conditions, 2 test dot speeds (2.5 deg s^{-1} and 5.0 deg s^{-1}) \times 6 inducing dot speeds ($1.25, 2.5, 3.75, 5, 6.25$, and 7.5 deg s^{-1}) \times 10 test-inducing motion direction separations ($\pm 30^\circ, \pm 60^\circ, \pm 90^\circ, \pm 120^\circ$, and $\pm 150^\circ$). Because the inducing stimulus parameters varied greatly in both direction and speed, potentially complicating the experimental task, we simplified the stimulus by having the trajectory of the test dot originating at the screen's centre in every trial. Further, because there were so many conditions, the single staircases

were terminated after 6 reversals and the last two were averaged. Step sizes were 5.0° , 2.0° , 1.0° , 1.0° , and 0.5° . There were twenty-one subjects drawn from the same population as those in experiment 1.

4.2 Results

Figure 6a shows the means and standard errors of illusory direction shifts when test dot speed was 2.5 deg s^{-1} and figure 7a shows the same for test dot speed of 5 deg s^{-1} . In both Figures 6a and 7a there is a clear ordering of direction shift magnitude as a function of inducing speed, confirming our first prediction. Figure 8 replots some of the data from figures 6a and 7a as direction errors for 2 test dot speeds and 3 test-to-inducer speed ratios as a function of inducer–test direction separation. From the figure legend it can be seen that the test-to-inducer speed ratio is 2.00 for the square symbols, 1.00 for the circular symbols, and 0.66 for the triangular symbols. Our second prediction was that direction shift functions for equal test-to-inducer speed ratios would be the same. This was confirmed through a multi-factorial analysis, which showed main effects of test-to-inducer speed ratio ($F_{2,40} = 103.42$, $p < 0.001$) but no main effect of test speed ($F_{1,20} = 1.74$, $p = 0.2$). There was also a main effect of direction difference ($F_{2,80} = 44.86$, $p < 0.001$).

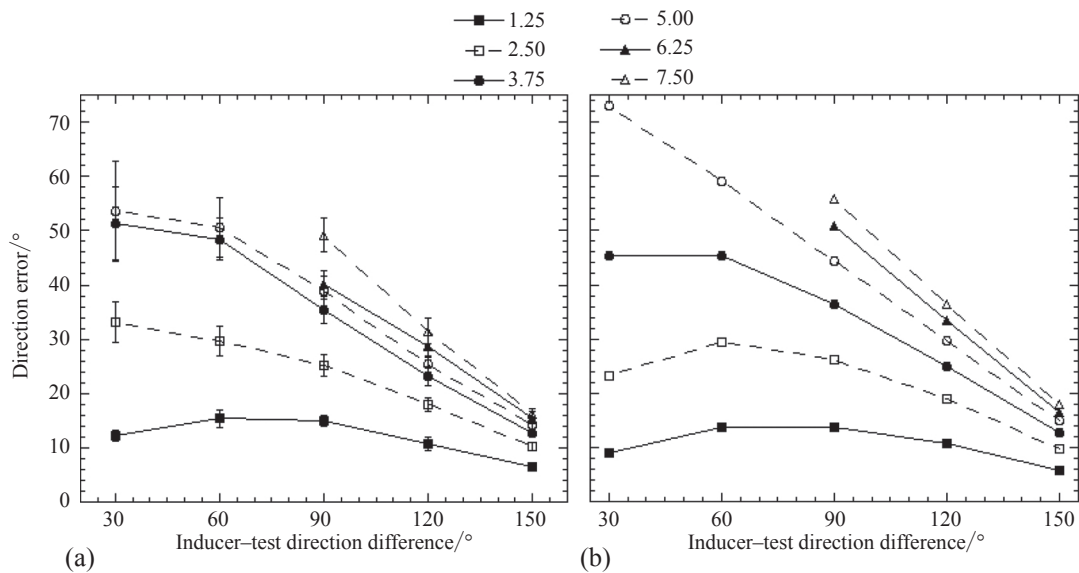


Figure 6. (a) Illusory direction shifts for the 2.5 deg s^{-1} test dot for 6 inducing speeds and 5 test-inducing direction differences (\pm direction differences averaged). (b) Illusory direction shifts for the 2.5 deg s^{-1} test dot predicted by the model $PT = T - k.I$, with the constant $k = 0.4907$.

There was a significant interaction between test-to-inducer speed ratio and direction separation ($F_{8,160} = 22.67$, $p < 0.001$), but not between test speed and direction separation ($F_{4,80} = 0.73$, $p = 0.58$) or between test speed and test-to-inducer speed ratio ($F_{2,40} = 2.40$, $p \leq 0.10$).

Our third prediction was that the peak shift in perceived direction would occur at smaller inducer–test directional differences as the test-to-inducer speed ratio was decreased. This was also confirmed by our results. In figures 6a, 7a, and 8, the higher test-to-inducer speed ratios produced peaks in direction shift S at direction differences of $\theta \sim 90^\circ$, and the peak in S appears to occur closer to $\theta = 0^\circ$ as the ratio is decreased.

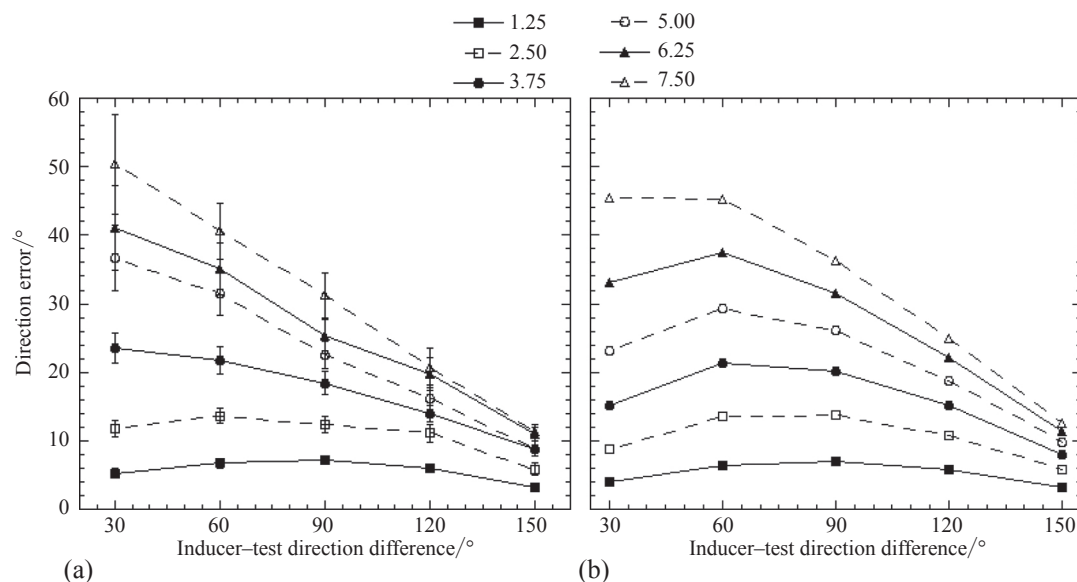


Figure 7. (a) Illusory direction shifts for the 5 deg s⁻¹ test dot for 6 inducing speeds and 5 test-inducing direction differences (\pm direction differences averaged). (b) Illusory direction shifts for the 5 deg s⁻¹ test dot predicted by the model $PT = T - k \cdot I$, with the constant $k = 0.4907$.

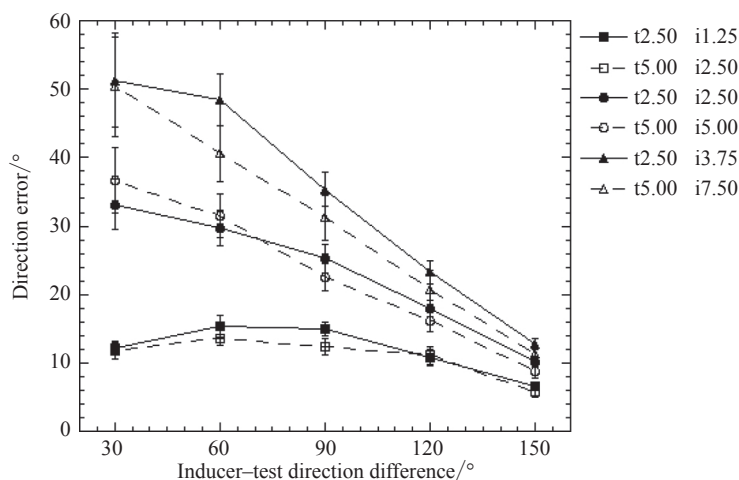


Figure 8. Some of the data from figures 6a and 7a replotted as direction errors for 2 test (t) dot speeds and 3 test-to-inducer speed ratios (2.0, 1.0, and 0.67) as a function of inducer-test direction separation.

5 Modelling

In experiment 1, we found that the results could be summarised by the model $PT = T - IM$. After measuring the shift in perceived direction across a range of inducing and test speeds, we have found that increasing the inducing speed increases IM. However, we found that our results could be very closely described by the model: $PT = T - k \cdot I$, where k is a constant and represents the ratio of IM to inducer speed.

Because the experimental design was not orthogonal, remembering that we omitted conditions with small test-to-inducer speed ratios and small direction differences from our experiment (see the introduction to experiment 2), we ran three separate analyses on our data.⁽¹⁾

⁽¹⁾ The data obtained from one observer were omitted because in one condition (test speed = 5 deg s⁻¹, inducer speed = 7.5 deg s⁻¹, direction separation = 120°) he/she produced an IM value of 121.52. The mean IM value for this condition was 8.452, and the standard deviation was 25.976. With the omission of that observer's data, the mean dropped to 2.798 and the standard deviation to 1.931.

For our first analysis, we conducted a 2 (test speed) $\times 4$ (inducer speed) $\times 5$ (inducer–test direction separation) repeated measures ANOVA. We ran the analysis on only 4 inducer speeds (1.25, 2.5, 3.75, and 5 deg s⁻¹), since the other two inducing speeds (6.25 and 7.5 deg s⁻¹) were not tested with the 2.5 deg s⁻¹ test speed at direction separations of 30° or 60°. We found that the mean IM-to-inducer speed ratio (k) averaged across inducer speeds and direction separations was 0.496 deg s⁻¹ (SE = 0.034) when the test speed was 2.5 deg s⁻¹ and 0.486 deg s⁻¹ (SE = 0.037) when the test speed was 5 deg s⁻¹. Our multi-factorial analysis showed the main effect for test speed to be non-significant ($F_{1,19} = 0.308$, $p = 0.585$). Combining the data from the two test speeds produced a mean IM-to-inducer speed ratio of $k = 0.491$ (SE = 0.034). There was, however, a significant interaction between direction difference and test speed ($F_{4,76} = 3.407$, $p = 0.013$), with the 5 deg s⁻¹ test speed producing a greater IM-to-inducer speed ratio than the 2.5 deg s⁻¹ test speed at a direction difference of 30° and the 2.5 deg s⁻¹ test speed producing a greater IM-to-inducer speed ratio than the 5 deg s⁻¹ test speed at a direction difference of 150°. The mean IM-to-inducer speed ratio averaged across test speeds and direction differences ranged from $k = 0.442$ for the 5 deg s⁻¹ inducing speed to $k = 0.533$ for the 1.25 deg s⁻¹ inducing speed. The main effect for inducing speed was significant ($F_{3,57} = 9.286$, $p < 0.0005$). The mean IM-to-inducer speed ratio averaged across test and inducer speeds ranged from $k = 0.450$ deg s⁻¹ to $k = 0.555$ deg s⁻¹ for the 5 direction differences. The main effect for direction difference was significant ($F_{4,76} = 5.372$, $p = 0.001$). In a second analysis, we ran a two-way repeated measures ANOVA on the 5 deg s⁻¹ test speed across 6 inducer speeds and 5 direction differences. As with the first analysis, significant main effects were found for both inducer speed ($F_{5,95} = 4.678$, $p = 0.001$) and direction difference ($F_{4,76} = 6.684$, $p < 0.0005$). The overall mean IM-to-inducer speed ratio was $k = 0.469$ (SE = 0.038). We also ran the following analysis: 2 test speeds (2.5 deg s⁻¹ and 5 deg s⁻¹), 6 inducer speeds (1.25, 2.50, 3.75, 5.00, 6.25, and 7.50 deg s⁻¹), and 3 direction differences (90°, 120°, and 150°). The overall mean IM-to-inducer speed ratio was $k = 0.447$ (SE = 0.034). Again, we found the main effect of test speed to be non-significant ($F_{1,19} = 1.611$, $p = 0.220$), and again we found the main effect of inducer speed to be significant ($F_{5,95} = 11.026$, $p < 0.0005$); however, the main effect of direction difference did not reach significance this time ($F_{2,38} = 2.256$, $p = 0.119$).

We calculated the overall mean value of k from all of our data: $k = 0.4907$. From our model, substituting in our calculated value k , we calculated predicted values of S that could then be compared to the experimental measurements of S that made up our data (compare figure 6b to figure 6a and compare figure 7b to figure 7a). To determine how good a fit our model provided, we ran a regression analysis, the results of which are plotted in figure 9. A regression analysis on the predicted values of S against the mean obtained values of S produced an R^2 value of 0.901. Our model therefore accounts for approximately 90% of the variance in the data means.

Since the proposed model accounted for 90% of the variance in the data means, 10% of the variance was left unexplained. This variance could quite possibly reflect a combination of noise due to errors in direction and speed discrimination (eg De Bruyn and Orban 1988; Gros et al 1998; Meng and Qian 2005) and to small but significant variation of k -values across the dependent variables. Variation of k -values could be the result of known perceptual asymmetries associated with differing veridical speeds and directions of motion. For example, speed acuity has been found to be optimal for speeds of between 4 deg s⁻¹ and 64 deg s⁻¹ (De Bruyn and Orban 1988). There is also evidence that oblique directions are perceived less accurately than are the cardinal directions (Loffler and Orbach 2001; Rauber and Treue 1998). Further, Lott and Post (1993) have found that IM is greater when the inducer moves upward than when it moves downward.

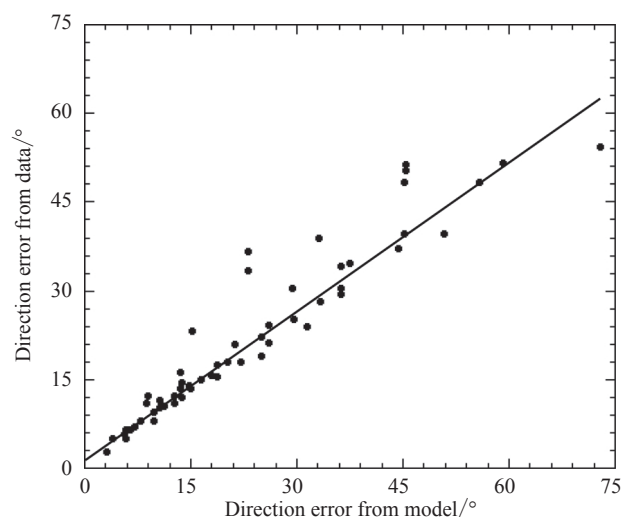


Figure 9. Means of obtained direction shifts across inducer–test direction differences (ordinate) plotted against direction shifts predicted by the model (abscissa). The regression line ($y = 2.3258 + 0.84865x$) indicates that the model $PT = T - kI$ when $k = 0.4907$ accounts for ~90% of the variance in the data ($R^2 = 0.901$).

Returning to experiment 1, from our results we calculated the mean IM-to-inducer speed ratio to be $k = 0.829 \text{ deg s}^{-1}$ ($SE = 0.035$), which is considerably larger than our value of $k = 0.4907 \text{ deg s}^{-1}$ obtained in the current experiment. We suggest that the difference reflects the slight configurational change that we introduced between the two experiments. The greater effect observed in experiment 1 may have resulted from the test stimulus originating at a point below the centre of the screen. As discussed in section 2.1.3, as the test dot approaches the top of the screen the effect is reduced by positional cues. Alternatively, changing the test dot's starting position from trial to trial in experiment 1 may have removed positional cues that were available in experiment 2, resulting in observers registering greater directional errors.

6 General discussion

Experiment 1 showed that whereas the angular function of the direction shifts due to the Zivotofsky (2004) Duncker-type illusion appeared to peak when the inducer–test separation was 90° , in fact the effect was so large that the data had to be replotted so that the x -axis showed the true inducer–test separation (figure 2). When this was done, the peak illusion occurred between 20° – 40° inducer–test separation, similar to the angular function of the motion direction illusion and aftereffect (see, for example, Wiese and Wenderoth 2007). We showed that the results could be summarised by the vectorial model $PT = T - IM$, and that $IM = 2.488 \text{ deg s}^{-1}$.

Experiment 2 tested predictions derived from vector diagrams (figure 3) that suggested that illusory direction shift magnitude would be determined by the ratio of test speed to inducer speed, with larger effects occurring when this ratio was smallest and with no effect of absolute test or inducer speed. We also tested the prediction derived from the vectorial relationships illustrated in figure 5 that the peak shift in perceived direction would occur at smaller inducer–test directional differences as the test-to-inducer speed ratio was decreased. All of these predictions were confirmed by our results (figures 6a, 7a, and 8).

While the peak effect appears to have occurred at an inducer–test separation of $\sim 30^\circ$ when the test and inducer speeds were equal, we found that the peak occurred at different inducer–test separations as the ratio of test-to-inducer speed was varied. This might at first seem incongruous with the suggestion that IM and the Duncker illusion share a common mechanism. However, since no studies have yet investigated the effects of the test-to-inducer speed ratio on the angular function of the DI, we cannot discount the possibility that it too would exhibit peak effects at various inducer–test separations depending on the relative

speed of the test and inducing stimuli. We therefore further conclude that there is no reason to believe that Zivotofsky's illusory direction shifts are qualitatively different from the DI and DAE. This conclusion is important because it suggests that the DI, the DAE, and the Zivotofsky illusion can probably be classified as similar illusory effects and may well have a common mechanism. In the absence of the replotted data in figure 2, the data gave the impression that whereas the DI and DAE exhibit peak effects at inducer-test separations of 20°–40°, the Zivotofsky effect peaks at 90° inducer-test separation. This in turn could easily mislead researchers into believing that the Zivotofsky effect has a mechanism completely different from that of the DI and the DAE.

In developing a model for the effects observed in experiments 1 and 2, we have found that the partial vector subtraction of the inducing velocity could account for nearly all of the variation in our data. This finding lends support to Gogel's (1979) vector-sum model of IM. Further, we have extended this model by showing that the vector subtraction can be calculated from the ratio of IM to inducer speed. The current findings are strongly indicative of the truth in the assumption that the observed shifts are the result of a one-dimensional induced speed shift in the opposite direction to the inducing motion. However, such a conclusion cannot be drawn with complete confidence until the perceived test speed is also measured. This will be the undertaking in a planned future study.

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Challenging the distribution shift: Statically-induced direction illusion implicates differential processing of object-relative and non-object-relative motion

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ABSTRACT

The direction illusion is the phenomenal exaggeration of the angle between the drift directions, typically, of two superimposed sets of random dots. The direction illusion is commonly attributed to mutual inhibition between direction-selective cell populations (distribution-shift model). A second explanation attributes the direction illusion to the differential processing of relative and non-relative motion components (differential processing model). Our first experiment demonstrates that, as predicted by the differential processing model, a static line can invoke a misperception of direction in a single set of dots – a phenomenon we refer to as the statically-induced direction illusion. In a second experiment, we find that the orientation of a static line can also influence the size of the conventional direction illusion. A third experiment eliminates the possibility that these results can be explained by the presence of motion streaks. While the results of these experiments are in agreement with the predictions made by the differential processing model, they pose serious problems for the distribution-shift account of shifts in perceived direction.

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1. Introduction

Our perception of the motion of an object is determined both by its spatial context and the motion of the object itself. An everyday example of the influence an object's spatial context has on its perceived motion comes from Rubin (1927), who described an observer's perception of a passenger waving with vertical hand movements from the window of a passing train. The observer does not perceive the passenger's hand tracing out a sine wave, which is its path of motion relative to the observer (veridical motion). Instead, the train becomes a perceptual frame of reference, and the hand is seen as oscillating vertically, relative to the train. Effects of spatial context on perceived motion have long been used in studies of the human visual system (e.g. Duncker, 1929/1955). One such effect, known as the direction illusion, is the phenomenal exaggeration of the angle between the respective directions of two stimuli translating in the frontoparallel plane (Marshak & Sekuler, 1979; Mather & Moulden, 1980). The direction illusion is typically observed in transparent motion displays, such as bidirectional random dot kinematograms (RDKs), which consist of two superimposed sets of random dots moving continuously, each in a different direction.

1.1. Distribution-shift model

The direction illusion is generally thought to arise from mutual inhibition between direction-selective cell populations that are most responsive to the two veridical directions in the display, as postulated by the distribution-shift model (e.g. Mather, 1980; Mather & Moulden, 1980) (Fig. 1A). The distribution-shift model is based on the premise that a stimulus moving in a constant direction in the frontoparallel plane evokes responses in a population of cells tuned to a continuum of directions of motion. The activity in these cells can be represented by an approximately Gaussian distribution, with its peak indicating the responses of cells tuned specifically to the stimulus' veridical direction, and its tapering flanks corresponding to the responses of cells tuned to increasingly divergent directions (e.g. Albright, 1984) (Fig. 1B). Cells that usually respond maximally to a given direction are inhibited when a second stimulus of a different direction is presented simultaneously (see Snowden et al., 1991). However, cells tuned to more divergent directions are less inhibited by the additional stimulus. The distributions thus become skewed, so that cells less affected by the inhibition are now the cells most responsive to the stimulus. As a result, the peaks of the two response distributions shift apart, invoking a percept of the two directions being more divergent than they actually are. Mutual inhibition thus distorts the perceived motion trajectories in a way that has been described as direction 'repulsion' (Marshak & Sekuler, 1979; Rauber & Treue, 1999; Raymond, 1993). The distribution-shift model is widely considered

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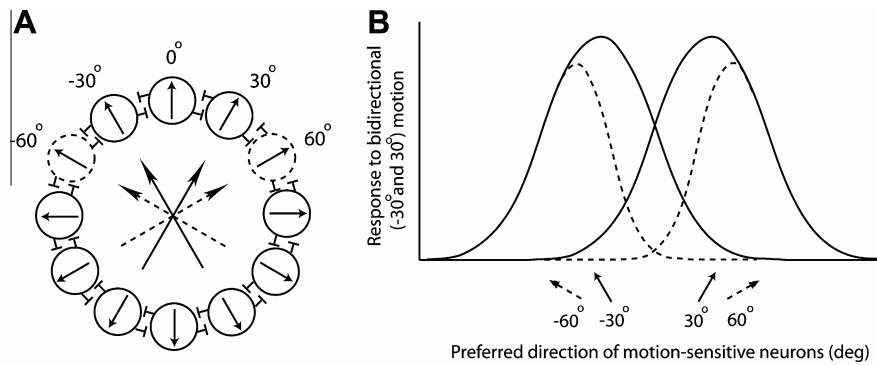


Fig. 1. Diagrams depicting the distribution-shift model (Mather & Moulden, 1980). (A) An explanation of direction repulsion as resulting from mutual inhibition between direction-selective cell populations (adapted from Hiris and Blake (1996)). When presented with a bidirectional (e.g. $\pm 30^\circ$) stimulus (solid central arrows), cells tuned to vertical are most inhibited, since these cells are equally responsive to either direction. The cells tuned maximally to the two stimulus directions are also inhibited to an extent so that the cells tuned to more divergent directions (dashed circular outlines) are now the most responsive, resulting in a perceptual exaggeration of the difference between the two directions (dashed central arrows). (B) The hypothetical responses (not to scale) of a population of direction-selective cells to a particular stimulus can be represented by a Gaussian distribution. When two directions ($\pm 30^\circ$) are presented simultaneously, activation of cells that respond to both directions is suppressed. The distributions thus become skewed, such that cells tuned to, say, -60° are now most responsive to the -30° stimulus. Thus, the population response to a -30° stimulus now evokes a percept of a stimulus moving at -60° .

as applying to the domain of motion direction. However, an essentially identical model was originally introduced to account for distortions in perceived orientation, namely the tilt illusion – the phenomenal exaggeration of the angle between two differently oriented static lines (Blakemore, Carpenter, & Georgeson, 1970). Like the direction illusion, the tilt illusion has been attributed to mutual inhibition, but between orientation- rather than direction-selective cell populations (Blakemore, Carpenter, & Georgeson, 1970; Carpenter & Blakemore, 1973; Wenderoth, O'Connor, & Johnson, 1986).

1.2. Differential processing model

Dakin and Mareschal (2000) argued that mutual inhibition between direction-selective channels does not explain certain aspects of the direction illusion, and they presented a variation of the phenomenon to demonstrate this. Two sets of dots with a direction separation of 45° would normally yield a large direction illusion (e.g. Grunewald, 2004; Marshak & Sekuler, 1979; Wiese & Wenderoth, 2007). Dakin and Mareschal found that including a third set of dots drifting at sufficient speed in a direction opposite to the vector average direction of the first two eliminated the effect. They asserted that the distribution-shift model makes no such prediction. However, there is a possible problem with discounting the distribution-shift model based on this finding alone. Although the third set was directionally distant from the other two sets ($\pm 157.5^\circ$, respectively), and although repulsion in many cases is found to persist only up to direction separations of $120\text{--}135^\circ$ (e.g. Grunewald, 2004; Marshak & Sekuler, 1979; Wiese & Wenderoth, 2007), Dakin and Mareschal (2000) themselves, in another experiment from the same paper, recorded significant repulsion with a direction separation of 135° . Moreover, we know that the greater the ratio of speeds for the two sets of dots (up to a ratio of $\sim 2:1$), the greater the shift in the slower set (Benton & Curran, 2003; Dakin & Mareschal, 2000; Kim & Wilson, 1996; Lindsey, 2001; Marshak & Sekuler, 1979). Hence, the possibility remains that, through mutual inhibition, the third set of dots was invoking counteractive angular repulsion on each of the other sets to cancel out the initial direction illusion. Notwithstanding this possibility, Dakin and Mareschal (2000) suggested that the phenomenon could be more adequately explained in terms of an alternative model. They proposed that the direction illusion results instead from the differential processing of two types of relative motion, similar to that described by Johansson (1950). Johansson (1950) contended

that the veridical velocity of an object is perceptually broken down into two component velocities: an object-relative component and a non-object-relative component. He described the object-relative component as the motion that is 'unique' to the object and the non-object-relative component as that which is 'common' to all objects in the visual field with respect only to the observer. Returning to Rubin's example, the veridical sinusoidal motion of the waving hand is parsed into object-relative and non-object-relative components, being respectively its vertical motion relative to the train and the horizontal motion common to both the train and the hand. Johansson further asserted that the non-object-relative component velocity provides a reference frame for the object-relative component velocity of each object. Accordingly, the hand in Rubin's example is perceived as oscillating vertically. Johansson demonstrated that this object-relative component is the 'dominant' percept, so that, for example, when two objects seen against a homogeneous background move at equal speed in orthogonal directions from a common point, they are perceived as moving directly away from each other. Orthogonal to this, the non-object-relative component is also detected but is perceptually 'secondary in character' and not always apparent (Johansson, 1950). According to Dakin and Mareschal (2000), differential processing can potentially account for the direction illusion in much the same way: if the non-object-relative component velocity is perceptually underestimated with respect to that of the object-relative component, the directional separation of the two sets of dots in a bidirectional RDK will be perceptually exaggerated (Fig. 2).

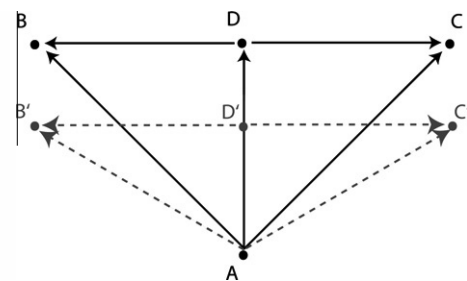


Fig. 2. Vector diagram of the differential processing account of the direction illusion. Vectors AB and AC represent the veridical trajectories of two sets of dots. The non-object-relative component AD is, with respect to the object-relative component velocities $B'D'$ and $D'C'$, perceptually underestimated, as AD' . This results in a perceptual exaggeration of $\angle BAC$ as $\angle B'AC'$ (adapted from Dakin and Mareschal (2000)).

1.3. Supporting evidence for differential processing

Johansson's work is descriptive rather than explanatory. However, empirical justification for postulating the differential processing model comes from numerous psychophysical studies showing that separate neural processes facilitate the extraction of object-relative and non-object-relative component velocities, and that our visual system is more responsive to object-relative than to non-object-relative motion. Velocity and displacement detection thresholds (Beardsley & Vaina, 2008; Lappin, Donnelly, & Kojima, 2001; Legge & Campbell, 1981; Leibowitz, 1955; Mack, Fisher, & Fendrich, 1975; Shioiri et al., 2002; Snowden, 1992; Sokolov & Pavlova, 2006) and reaction times (Smeets & Brenner, 1994), for example, are lower for object-relative than for non-object-relative motion perception. Changes in stimulus luminance contrast have been found to differentially affect detection of object-relative and non-object-relative velocities. Grossman and Blake (1999) used an RDK to investigate the effects of low and high luminance conditions on object-relative and non-object-relative motion. Detection of object-relative motion required detection of a region within the RDK defined by the offset trajectories of a number of dots as they moved over the area. They found that while low luminance levels impaired the detection of object-relative motion, they did not diminish detection of non-object-relative motion. In another study, Levinson, Coyne, and Gross (1980) found that when contrast was reduced to peri-threshold levels, a bi-directional RDK with an angular separation of 30° was seen as a single sheet of dots moving in a direction midway between the two component directions. The reported percept therefore corresponded with observers perceiving the non-object-relative component motion only, showing again that object-relative and non-object-relative motion perception are differentially affected by changes in contrast. Moreover, the speed of a stimulus in non-object-relative motion has been found to be perceptually underestimated in comparison to one viewed in object-relative motion (Blakemore & Snowden, 2000; Brown, 1931; De Bruyn & Orban, 1999; Gogel & McNulty, 1983; Nguyen-Tri & Faubert, 2007; Norman et al., 1996). Brown (1931) compared the perceived velocity of dots moving against a homogeneous background with dots moving against a textured background and found the latter to appear 25% faster. Gogel and McNulty (1983) found increases of up to 42% in the perceived speed of a translating spot of light as the density of reference cues was increased from 0.1 to 0.65 marks/cm. Similar results have been reported in a subsequent study (Ornan, 2009). Norman et al. (1996) found that the perceived speed of a central region of random dots was higher in the presence of a surrounding region of stationary dots than when the stationary dots were absent. Blakemore and Snowden (2000) found that a dot moving across a high-contrast background appears faster than a dot moving across a low-contrast background. De Bruyn and Orban (1999) compared the perceived speed of a set of dots when presented alone and when in transparent motion with a second set of dots moving in the opposite direction. The perceived speed was found to be 50% greater in the transparent motion condition. All of these studies indicate that objects viewed in object-relative motion are perceived as being faster than objects of equal veridical speed viewed in non-object-relative motion. Taken together, the results from the above studies constitute ample justification for considering the differential processing of object-relative and non-object-relative component velocities as a possible mechanism underlying the contextual determination of perceived stimulus direction, as in the case of the direction illusion.

1.4. Current objectives

The aim of the current paper was to evaluate and compare the adequacy of both the distribution-shift and differential processing

models in accounting for the perception of stimulus direction. To this end, taking a similar approach to Dakin and Mareschal (2000), we presented new variations of the conventional direction illusion-invoking stimulus configuration that allowed distinct predictions to be made by each model. Specifically, we investigated the effects of a static line stimulus on the perceived direction of a unidirectional set of dots (Experiment 1), as well as on the perceived direction of one of the sets of dots in a bidirectional direction illusion-invoking display (Experiment 2). We also investigated whether a more broadly defined distribution-shift model might account for the results (Experiment 3).

2. Experiment 1

When the endpoints of a moving line are obscured, such as when it is viewed through a circular aperture, the line will appear to move in a direction orthogonal to its orientation, since the endpoints provide the only cue to any motion of the line parallel to its orientation. This is the well-known 'aperture problem' (Wallach, 1935). The same effect can be achieved without the aperture if the endpoints can be otherwise obscured, such as if the line extends beyond a certain eccentricity, particularly if the line's contrast is tapered towards its endpoints, since the visual system has a lower acuity and higher contrast detection threshold for stimuli in the periphery (see Anstis, 2003). Similarly, such a line, if presented as a stationary reference for other moving elements, will provide no positional reference cues along the axis of its orientation. Since object-relative motion by definition requires reference points and non-object-relative motion by definition requires the absence of reference points, any motion orthogonal to that axis will be object-relative and (in the complete absence of all other visual references) any motion parallel to that axis will be non-object-relative motion. The differential processing model dictates that any unidirectional motion oblique to the line will be parsed by the visual system into a non-object-relative component parallel to the line and an object-relative component orthogonal to the line. Further, because of the visual system's greater responsivity to object-relative than to non-object-relative motion, the velocity component parallel to the line (non-object-relative) will be perceptually reduced in comparison to that orthogonal to the line (object-relative). The direction of a stimulus such as a set of dots drifting obliquely to the line should therefore be shifted perceptually towards the orthogonal, i.e. the direction of the dots should be 'repelled' by the orientation of the line (Fig. 3). This predicted shift in perceived direction of a single set of dots invoked by the presence of the static line we will refer to as the statically-induced direction illusion. The distribution-shift model, on the other hand, makes no such prediction since, by definition, it requires the presence of two directions of motion. The current experiment was designed to test for the occurrence of a statically-induced direction illusion and, if one was observed, to ascertain how the angular difference between the orientation of the inducing line and the test direction affects the magnitude of the illusion. This would enable us both to draw comparisons with previously obtained angular functions of the conventional direction illusion and to determine the optimal stimulus parameters for use in later experiments.

2.1. Method

2.1.1. Apparatus

All stimuli were generated and presented and all responses recorded with Psykinematix version 1.1.0 (build 1011) (KyberVision, Montreal, Canada, psykinematix.com). The software was run on a G5 Macintosh Dual 2 GHz Power PC running Mac OS X version 10.4.11. The SONY Trinitron Multiscan G520 monitor had a frame

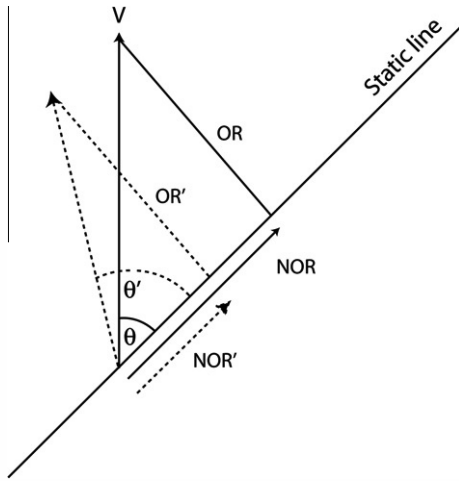


Fig. 3. The dissociation of object-relative (OR) and non-object-relative (NOR) component velocities of a drifting stimulus due to the presence of a stationary line. The veridical velocity (V) is vertically upward, while its object-relative and non-object-relative component velocities are respectively orthogonal and parallel to the static line. We hypothesise that the non-object-relative component velocity will be perceptually underestimated (as NOR') with respect to the object-relative component, resulting in the angular separation of the drifting stimulus direction and the orientation of the line (θ) being perceptually exaggerated (θ').

refresh rate of 75 Hz and a pixel resolution of 1152×870 . Participants viewed the screen binocularly from a distance of 57 cm through a cylinder (diameter 30 cm, length 57 cm) that was lined internally with matte black felt, and a chin and headrest prevented head movement.

2.1.2. Stimuli

A unidirectional white-on-grey RDK (test stimulus) comprising a coherently drifting set of 40 Gaussian dots was presented within an 8-deg virtual aperture with no visible boundary. All dots had a peak luminance of 104 cd/m^2 , with a standard deviation of 6 min-arc and a drift speed of 0.5 deg/s . The background luminance was 65 cd/m^2 , giving a Michelson contrast of 23.1%. Dependent upon each observer's responses, the test stimulus drifted in a range of directions close to upward vertical (0°). The inducing stimulus was a static white line (length 27.78 deg, and width 0.12 deg) whose midpoint was located in the centre of the display. The luminance profile along the line's length followed a sin curve (0.018 cpd) with maximum contrast (23.1%) at the line's midpoint, decreasing to 0% contrast at each endpoint. The line was presented at one of seven orientations (3° , 7.5° , 15° , 30° , 45° , 60° , 75° , and 90°) relative to the test direction (positive values indicate clockwise (CW) directions). A baseline condition incorporating an RDK but no inducing line was also presented.

2.1.3. Observers

Twenty-two 2nd-year psychology students at Macquarie University completed the experiment. All were inexperienced observers and none were aware of the purpose of the study. All were emmetropic or had corrected-to-normal vision.

2.1.4. Procedure

Each trial began with a brief tone and a 500 ms presentation of a uniform grey field with a small point in the centre of the screen. Test stimuli were then presented for 500 ms, during which time the central point was not present. Observers were instructed to remain fixated as near as possible to where the point had initially been presented. Being the centre of the display, this point coincided with the midpoint of the static line. Each successive trial

began once a response was made. The seven test conditions were fully randomised within a single block of trials. The baseline condition was run in a separate block. This study used a standard staircase method (Wetherill & Levitt, 1965) to estimate each observer's point of subjective vertical. Observers indicated, using the left and right arrow keys, which side of upward vertical (0°) they perceived the test stimulus to be moving. Observers completed two randomly interleaved 1-up-1-down staircases with respective starting values of $\pm 10^\circ$ from vertical, for each condition. Initial step size was 5° , reducing to 4° , 3° , 2° , and a minimum of 1° on subsequent reversals. Each staircase terminated after 12 reversals, with the direction of the test stimulus on the final 6 reversals from each staircase being averaged for each observer to serve as an estimate of perceived vertical. Obtained means were adjusted by subtracting individual values of perceived vertical measured in the baseline condition.

2.2. Results and discussion

The results from Experiment 1 are reported in Fig. 4. Directional shifts were small or absent when test/inducer separations were either very small ($\leq 15^\circ$) or very large (90°). However, intermediate separations yielded large CCW shifts in perceived direction. A set of one-sample two-tailed t -tests showed CCW shifts significantly different from zero for each of the 30° , 45° , 60° , and 75° conditions ($t_{(19)} \geq 6.43$, $p < 0.0005$, $\eta^2 \geq 0.685$), and no significant shift for the 3° , 7.5° , 15° , or 90° conditions ($t_{(19)} \leq 2.29$, $p \geq 0.034$) (p -values were Bonferroni-adjusted to control for overall error rate). Two of the observers produced anomalous data that indicated an obvious inability or reluctance to follow the instructions. Their data were therefore omitted from the analysis.

The primary aim of the current experiment was to test for the occurrence of a statically-induced direction illusion, which we found. Since mutual inhibition between direction-selective channels could only occur when two directions of motion are presented together, the illusions observed here cannot be accounted for by the distribution-shift model. On the other hand, the occurrence of the phenomenon is predicted by the differential processing model. The peak illusory effect was only $\sim 10^\circ$, while the peak effect obtained in most direction illusion studies is $\sim 20^\circ$ (Grunewald, 2004; Hiris & Blake, 1996; Marshak & Sekuler, 1979; Mather & Moulden, 1980; Rauber & Treue, 1998; Wiese & Wenderoth, 2007) (see also our results from Experiment 2). Discrepancies between the angular functions of the statically-induced direction

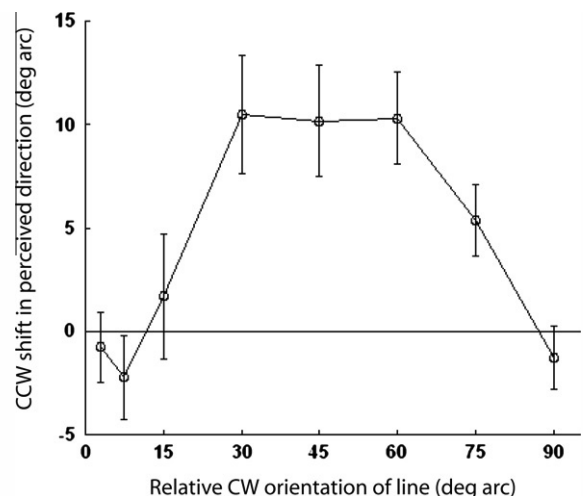


Fig. 4. Graph showing the results of Experiment 1. Error bars represent 95% confidence intervals.

illusion and those previously reported for the conventional direction illusion are not surprising, however, due to the differences between the stimuli used to invoke the respective illusions.

3. Experiment 2

Having demonstrated the existence of a statically-induced direction illusion, we wished to determine whether the magnitude of a conventional direction illusion could be increased and/or reduced by including differently orientated visual reference cues in the display. Here, we investigated the effects of the orientation of a static line on the perceived direction of one of the sets of dots in a bidirectional RDK.

According to the logic of the differential processing account, the introduction of a static line oriented parallel to the object-relative component velocity direction in a bidirectional RDK (parallel to BC in Fig. 2), will provide a reference cue for motion in the non-object-relative component direction (AD in Fig. 2), transforming what was initially non-object-relative motion into object-relative motion. What was initially the object-relative component velocity should be unaffected since the line does not introduce any further reference for motion along its axis. The line should therefore diminish the size of the direction illusion. Conversely, a line parallel to the non-object-relative component velocity should not affect the direction illusion magnitude, since a line with such an orientation would provide no reference along the axis of the non-object-relative component velocity. It would only provide an additional reference along the axis of the object-relative component velocity where references cues are already available. However, there is a possibility that the additional reference will slightly increase the object-relative component velocity, thereby marginally increasing the size of the direction illusion.

The distribution-shift model, however, contends that the mutual inhibition that arises in a bidirectional RDK is driven by the veridical velocities of the two sets of dots invoking responses in direction-selective channels. As these units show no response to stationary features, this model cannot predict that the presence of a static line of any orientation should have an influence on the magnitude of the direction illusion.

The current experiment was designed to determine whether or not the magnitude of the direction illusion observed in a bidirectional RDK would be reduced by the presence of a static line oriented orthogonally to the non-object-relative component velocity, and either increased or unaffected with the line oriented parallel to the non-object-relative component velocity.

3.1. Method

The apparatus was identical to that in Experiment 1, but several changes were made to the stimulus configuration. Here we used bidirectional RDKs with one set of dots considered the test stimulus and the other the direction illusion inducer, which drifted at 30° relative to the test direction. The 30° direction separation was chosen on the basis that the same separation yielded the largest statically-induced direction illusion in Experiment 1. The experiment included three conditions, one of which consisted of the bidirectional RDK alone (Fig. 5A), and two of which also incorporated the static white line, which was oriented at either -75° or 15° relative to the test direction (see Fig. 5B and C). The two orientations were specifically selected to match the direction of the object-relative and non-object-relative component velocities, respectively. The three test conditions were fully randomised within a single block of trials. Obtained means were adjusted by subtracting individual values of perceived vertical measured in the baseline condition in Experiment 1.

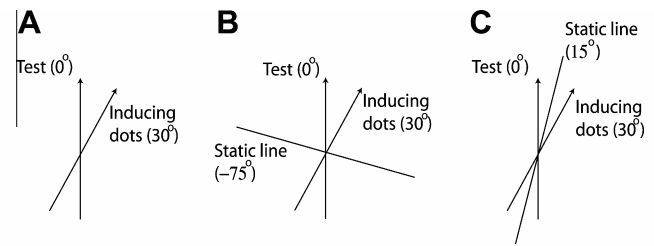


Fig. 5. Schematic diagram of the three test conditions in Experiment 2: (A) Bidirectional RDK with test direction 0° and inducing dots direction 30° relative to test direction. (B) Bidirectional RDK with a static line oriented at -75° relative to the test direction, i.e. aligned with the object-relative component velocities. (C) Bidirectional RDK with a static line oriented at 15° relative to the test direction, i.e. aligned with the non-object-relative component velocity.

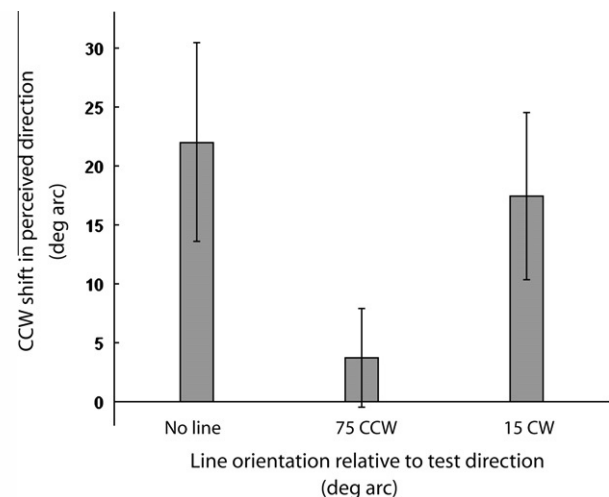


Fig. 6. Graph showing the results of Experiment 2. Error bars represent 95% confidence intervals.

3.1.1. Observers

Twenty-one of the 22 observers who participated in Experiment 1 also participated in Experiment 2.

3.2. Results and discussion

Data from five of the observers, including those omitted in Experiment 1, were omitted from the current analysis, the reason being that three observers produced results in the direction illusion condition indicating a CW shift in perceived direction, opposite to the expected shift.¹ Results from Experiment 2 are reported in Fig. 6. For the no-line (direction illusion) condition we obtained a mean CCW directional shift of 22.0° , which is similar in size to previous measurements of the direction illusion with the same directional separation of 30° (Braddick, Wishart, & Curran, 2002; Grunewald, 2004; Rauber & Treue, 1999; Wiese & Wenderoth, 2007). With a line oriented at 75° CCW of the test direction we obtained a mean CCW directional shift of 3.7° , and with a line oriented at 15° CW of the test direction we obtained a mean CCW directional shift of 17.4° . A set of one-sample two-tailed *t*-tests showed the direction illusion in the no-line condition ($t_{(15)} = 5.511$, $p < 0.0005$,

¹ The aim of our study was to compare the capacity of two models to predict characteristics of the direction illusion as it is generally observed. As no previous study has reported an attraction effect when the inducer and test directions are separated by 30° , we considered it prudent to omit these data. However, when these results are included, there is no appreciable change in the pattern of results obtained, or in the statistical significance of the findings.

$\eta^2 = 0.669$), and in the 15° CW condition ($t_{(15)} = 5.203$, $p < 0.0005$, $\eta^2 = 0.643$) to be significantly different from zero. However, the small shift in the 75° CCW condition was not significantly different from zero ($t_{(15)} = 1.861$, $p = 0.082$), signifying that the presence of the line in this condition was effective in eliminating the direction illusion. Two-tailed t -tests showed a significant difference between the no-line and 75° CCW condition ($t_{(15)} = 6.806$, $p < 0.0005$) but no significant difference between the no-line and 15° CW condition ($t_{(15)} = 1.432$, $p = 0.173$).

While the results of the no-line and 15° CW conditions are consistent with a distribution shift, the model cannot account for the results of the 75° CCW condition. On the other hand, the results of all three conditions are readily interpretable if we attribute the direction illusion to differential processing. As predicted by this model, the direction illusion was significantly reduced in the 75° CCW condition, possibly because the non-object-relative component velocity is no longer underestimated when the line is added, since the line effectively transforms this component into an object-relative motion. The direction illusion was unchanged by the presence of the 15° CW line. We can infer from this finding that the object-relative component velocity was unchanged by the additional reference cue.

4. Experiment 3

As described earlier, the distribution-shift model attributes the direction illusion to mutual inhibition between direction-selective cell populations. The previous two experiments have respectively demonstrated the inability of this model to account for the capacity of a static line to invoke a direction illusion (Experiment 1) and to eliminate the direction illusion in a bidirectional RDK (Experiment 2). One way in which we might attempt to reconcile these findings with the distribution-shift model is by considering the possible involvement of mutual inhibition not between direction-selective channels but between orientation-selective channels. We will refer to this proposed mechanism as an orientation distribution shift. Geisler (1999) proposed that moving stimuli produce neural ‘motion streaks’ within the visual system. He suggested that motion streaks should result from the temporal integration of motion signals activating orientation-selective neurons that are tuned to orientations parallel to the direction of motion. If motion stimuli could activate orientation-selective channels, then we should expect to observe perceptual interactions between direction and orientation domains. Geisler provided evidence for the occurrence of motion streaks by measuring the luminance detection threshold of a moving Gaussian dot as a function of its size and speed when it was presented with a grating mask at various orientations relative to the dot direction. When the dot moved above a certain critical speed of approximately 1 ‘dot width’ per 100 ms (a dot width was defined as four times the dot’s Gaussian standard deviation) a parallel mask was significantly more effective in elevating thresholds than was an orthogonal mask, with intermediate mask orientations producing intermediate threshold elevations. Geisler found further evidence for the occurrence of motion streaks in an orientation adaptation experiment. After adaptation to a grating oriented 10° from vertical, observers judged the direction of a vertically moving 12-min dot. The dot had a speed of either 2.5 or 10 deg/s, which according to Geisler’s estimations should produce, respectively, weak and strong motion streaks. While the faster dots showed a shift of $\sim 2.2^\circ$ in perceived direction, the slower dots were perceptually shifted by only $\sim 0.4^\circ$. The former result is comparable in size to the tilt aftereffect, which is a repulsive shift in the orientation of a line or grating due to previous adaptation to a differently oriented line or grating (e.g. Gibson & Radner, 1937). Apthorp and Alais (2009) produced further evidence of motion streaks activating

orientation-selective channels by showing a similar shift in the perceived orientation of a central grating due to simultaneously presented RDK motion surrounding the grating. They obtained an angular function for the effect, which we refer to hereafter as a motion-induced tilt illusion. The results were very similar to those produced in studies of the tilt illusion, which was defined in Section 1.1 (O’Toole & Wenderoth, 1977; Over, Broerse, & Crassini, 1972). Further evidence for direction/orientation interactions comes from studies using static configurations of paired dots that, when flashed in succession, invoke motion percepts whose direction is determined by the orientation of the dot pairs (e.g. Burr & Ross, 2002; Johnson & Wenderoth, 2011; Ross, Badcock, & Hayes, 2000).

The statically-induced direction illusions observed in Experiment 1 are an order of magnitude larger than the direction and orientation shifts associated with the occurrence of motion streaks. Also, in Experiments 1 and 2 we selected values for dot width and speed that would not meet the criteria for producing motion streaks. Remembering that the critical speed is calculated as 1 ‘dot width’ per 100 ms and that a dot width is defined as four times the dot’s Gaussian standard deviation, for a Gaussian dot with a standard deviation of 6 minarc, the ‘dot width’ is 24 minarc. The critical speed was thus 24 minarc per 100 ms, or 4 deg/s. We are therefore confident that the observed effects were not produced, at least not entirely, by this mechanism. However, we wanted to address directly the possible involvement of motion streaks in the production of the statically-induced direction illusion. To this end, we compared the size of the illusion when invoked with RDKs with speeds above and below the critical speed for producing motion streaks. If the illusion is due, at least in part, to mutual inhibition between orientation-selective channels responding to both the static line and motion streaks produced by the drifting dots, i.e. to an orientation distribution shift, we would expect to obtain a larger illusion with the faster dots than with the slower dots. The differential processing model, on the other hand, makes no specific predictions regarding the effects of speed. A further objective was to determine whether the RDK invokes a motion-induced tilt illusion in the static line. If the statically-induced direction illusion arises from an orientation distribution shift due to the presence of motion streaks, we should expect to observe a motion-induced tilt illusion and, as with the statically-induced direction illusion, it should be larger with faster dots than with slower dots. If the statically-induced direction illusion arises entirely from differential processing, however, no motion-induced tilt illusion is expected.

4.1. Methods

4.1.1. Apparatus and stimuli

The apparatus was the same as that used in Experiments 1 and 2. The stimuli differed from those in Experiments 1 and 2 as follows: Here the Gaussian dots had a standard deviation of 3 minarc. Drift speed was either slow (0.5 deg/s) or fast (8 deg/s), respectively below and above the critical speed of 2 deg/s required to produce motion streaks. In the statically-induced direction illusion conditions, the static line was always oriented at 30° relative to the direction of the RDK, and in the motion-induced tilt-illusion conditions, the direction of the RDK was always 30° relative to the orientation of the line.

4.1.2. Observers

Five observers, three male and two female, took part in the experiment. We were confident in using a small group of participants, because the task was relatively simple, and because a pilot study produced robust outcomes. Four of the observers were staff or students at Macquarie University and had previous experience with similar experimental tasks. One participant was the author, and one other was aware of the purpose of the experiment. One

observer had had no previous experience. All were emmetropic or had corrected-to-normal vision.

4.1.3. Procedure

We used four test conditions, labelled SDI slow (statically-induced direction illusion with slow-moving dots), SDI fast (statically-induced direction illusion with fast-moving dots), MTI slow (motion-induced tilt illusion with slow-moving dots), and MTI fast (motion-induced tilt illusion with fast-moving dots). We also ran three baseline conditions: the two statically-induced direction illusion conditions with the static line absent and a motion-induced tilt illusion condition with the RDK absent. In the direction illusion conditions observers judged the direction of the RDK, and in the tilt illusion conditions they judged the line's orientation. The seven conditions were run in separate blocks, which were presented in random order. The procedure was similar to that in Experiments 1 and 2. In each of the experimental conditions, observers completed two randomly interleaved staircases with starting values of $\pm 20^\circ$ from vertical. Initial step size was 32° , and was halved for each subsequent reversal, with a minimum step size of 1° . Obtained values for each condition were averaged for each observer and adjusted by subtracting individual values obtained from the corresponding baseline conditions.

4.2. Results and discussion

Results from Experiment 3 are reported in Fig. 7. For the SDI slow condition we obtained a mean CCW directional shift of 13.47° , which is comparable in size to that observed in Experiment 1, and in the SDI fast condition we obtained a mean CCW shift of 2.56° . One-sample two-tailed t -tests showed a significant difference from zero for each of the SDI slow ($t_{(4)} = 7.763$, $p = 0.001$, $\eta^2 = 0.938$), and SDI fast ($t_{(4)} = 7.034$, $p = 0.002$, $\eta^2 = 0.925$) conditions. A paired t -test showed there was a significant difference in the directional shift between the SDI slow and SDI fast conditions ($t_{(4)} = 6.463$, $p = 0.003$, $\eta^2 = 0.913$). For the MTI slow condition we obtained a mean directional CW shift of 0.03° , and in the MTI fast condition we obtained a mean CW shift of 0.06° . One-sample two-tailed t -tests showed no significant difference from zero for either the MTI slow ($t_{(4)} = 0.059$, $p = 0.956$) or MTI fast ($t_{(4)} = 0.098$, $p = 0.926$) conditions.

Our failure to observe a motion-induced tilt illusion in either the MTI slow or MTI fast condition indicates either that no motion streaks are produced by our drifting dot stimuli, or that motion streaks are produced but fail to affect the perceived orientation of the line. If the former is the case, then we can immediately

discount the involvement of an orientation distribution shift in producing the statically-induced direction illusion. If the latter is the case, there remains the possibility that the statically-induced direction illusion is produced by an orientation distribution shift but that the shift is asymmetrical, affecting the perceived orientation of the motion streaks, and therefore the perceived direction of the dots, without affecting the perceived orientation of the line. The SDI slow condition yielded a significant shift in perceived direction, indicating that the illusion is not due to the presence of motion streaks, as stimuli at this speed are incapable of forming any such features. Moreover, the shift was an order of magnitude larger than previously reported direction and orientation shifts associated with the interaction of motion streaks and static oriented stimuli (e.g. Aphorpe & Alais, 2009), indicating again that the effects shown in the current study cannot be explained in this way. Conversely, the stimuli in Experiment 3 that were predicted to produce strong motion streaks (SDI fast condition) in fact produced a very much reduced direction illusion. That the SDI slow condition produced a much larger shift than the SDI fast condition clearly contradicts the predictions of the orientation distribution-shift hypothesis and indicates that the statically-induced direction illusion does not arise from the mutual inhibition of orientation-selective cell populations resulting from the occurrence of motion streaks. In contrast, none of the conditions produced data that conflict with the differential processing model. The model makes no predictions of any orientation shift in either of the motion-induced tilt illusion conditions. Further, the SDI slow and SDI fast data are not inconsistent with the differential processing model. Although differential processing explicitly predicts a statically-induced direction illusion in both slow and fast conditions, it makes no specific quantitative prediction regarding the effect of dot speed and, in particular, the relative size of the effects in slow and fast conditions. Further research into the effects of speed on both object-relative and non-object-relative velocities is required before the model can be extended to make any such predictions. However, the current findings echo those previously reported in the context of the direction illusion. Our data show an increase in statically-induced direction illusion magnitude as the RDK speed is reduced from 8 deg/s to 0.5 deg/s. Rauber and Treue (1999) and Braddick, Wishart, and Curran (2002) also found that reducing the speed of both sets of dots in a bidirectional RDK increased the size of the conventional direction illusion considerably. The inverse relationship reported here of stimulus speed to the size of the shift in perceived direction is thus consistent with the proposal that the statically-induced direction illusion and the conventional direction illusion share a common mechanism.

5. General discussion

Dakin and Mareschal (2000) argued that mutual inhibition between direction-selective channels does not explain certain aspects of the direction illusion and proposed instead that the phenomenon arises as a result of the differential processing of object-relative and non-object-relative motion components. Without evidence solid enough to refute the distribution-shift model (see Section 1.2), however, subsequent studies have continued to attribute the direction illusion to mutual inhibition between direction-selective channels (e.g. Braddick, Wishart, & Curran, 2002; Chen, Matthews, & Qian, 2001; Curran, Clifford, & Benton, 2006, 2009). The primary aim of the current paper was to evaluate and compare the tenability of the distribution-shift and differential processing models of direction perception, particularly as they apply to the direction illusion. In Experiment 1, we observed a statically-induced direction illusion, an effect predicted by the differential processing model but not by the distribution-shift model. In Experiment 2, we found that

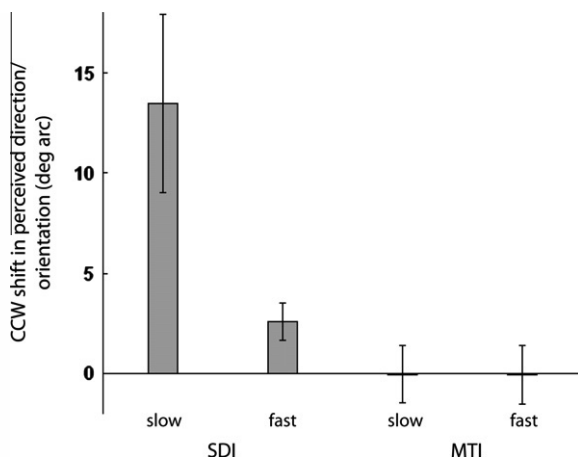


Fig. 7. Graph showing the results of Experiment 3. Error bars represent 95% confidence intervals.

introducing a static line parallel to the object-relative component direction of a direction illusion-invoking bidirectional RDK eliminated the illusion, while a line parallel to the non-object-relative component had no effect on the illusion. Again, the results are consistent with differential processing but not with mutual inhibition between direction-selective channels. In Experiment 3, we investigated the possibility that the results of Experiments 1 and 2 may be accounted for by the distribution-shift model applied to the orientation domain, hypothesising that the statically-induced direction illusion might arise from mutual inhibition between orientation-selective channels due to the existence of motion streaks. We measured the illusion with slow and fast moving dots and found the former to produce a larger effect. We also tested for the occurrence of a motion-induced tilt illusion due to slow and fast dot motion but found no effect. The results conflicted with the orientation distribution-shift hypothesis but were consistent with the differential processing model.

5.1. A third model – the clustering algorithm

One group of researchers (Mahani, Carlsson, & Wessel, 2005) has argued against the distribution-shift model, suggesting instead that the direction illusion occurs as a direct consequence of solving the motion transparency problem. They claim that implementation of a particular clustering algorithm, an iterative statistical process that is required to estimate the direction and group identity of the individual dots, necessarily leads to an exaggeration of the directional difference between the two dot sets. In other words, the direction illusion is a statistically inevitable by-product of the process of integration and segmentation of the independent elements in transparent motion. The results of Experiments 1 and 3, however, clearly demonstrate that directional shifts occur without any need for group identification since there was only one group present. In addition, the direction illusion was eliminated in Experiment 2 by the orientation of a static line, a result on which the clustering algorithm is silent. As such, the current results cannot be accounted for by the model of Mahani, Carlsson, and Wessel (2005).

5.2. Conclusion

We have shown that a static line can invoke shifts in the perceived direction of a moving stimulus and can eliminate the directional shift observed in a conventional direction illusion-inducing configuration. We have further shown that the direction shifts invoked by the static line cannot be explained by the existence of motion streaks. These findings cannot be attributed to a distribution shift resulting from mutual inhibition between either direction-selective or orientation-selective channels, and they pose serious questions about the distribution-shift model's adequacy in accounting for perceived direction in general. Conversely, the results reported here are consistent with the occurrence of differential processing of object-relative and non-object-relative component velocities by the visual system. Since moving objects usually have veridical velocities that comprise both types of motion, and since the latter type has been found to be underestimated with respect to the former, the differential processing model dictates that the perceived direction of such objects will be shifted from the veridical. We will be assessing the tenability of this model further in a future study on the effects of such processes on perceived stimulus velocity, i.e. direction and speed.

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The hierarchical order of processes underlying the direction illusion and the direction aftereffect

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Abstract. Motion perception involves the processing of velocity signals through several hierarchical stages of the visual cortex. To better understand this process, a number of studies have sought to localise the neural substrates of two misperceptions of motion direction, the direction illusion (DI) and the direction aftereffect (DAE). These studies have produced contradictory evidence as to the hierarchical order of the processing stages from which the respective phenomena arise. We have used a simple stimulus configuration to further investigate the sequential order of processes giving rise to the DI and DAE. To this end, we measured the two phenomena invoked in combination, and also manually parsed this combined effect into its two constituents by measuring the two phenomena individually in both possible sequential orders. Comparing the predictions made from each order to the outcome from the combined effect allowed us to test the tenability of two models: the DAE-first model and the DI-first model. Our results indicate that DAE-invoking activity does not occur earlier in the motion processing hierarchy than DI-invoking activity. Although the DI-first model is not inconsistent with our data, the possible involvement of non-sequential processing may be better able to reconcile these results with those of previous studies.

Keywords: direction illusion, direction aftereffect, direction repulsion, transparent motion, sequential processing

1 Introduction

Motion perception defines our spatiotemporal visual experience, although it is not always reliable. Instances in which motion is misperceived offer unique opportunities for studying the mechanisms involved in motion processing. The current paper investigates the hierarchical order of neural processes underlying two misperceptions of motion direction, the direction illusion (DI) (Marshak and Sekuler 1979; Mather and Moulden 1980) and the direction aftereffect (DAE) (Levinson and Sekuler 1976). The DI is an illusory exaggeration of the angle between the respective directions of two moving stimuli. It has often been studied with transparent motion displays, typically bidirectional random dot kinematograms (RDKs), which consist of two superimposed sets of random dots each scrolling continuously in a different direction (figure 1). The DI is usually measured as the shift in perceived direction of one set of dots (test) due to the presence of the other set (inducer). The DAE is a shift in perceived direction that occurs in one stimulus after adaptation to another stimulus moving in a different

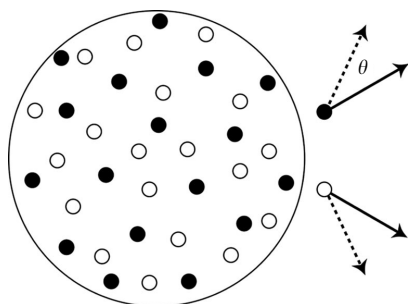


Figure 1. Schematic diagram of the direction illusion (DI): Black and white dots in the diagram represent the two random-dot sets, which are both white in the actual display. Solid and dotted arrows indicate, respectively, their physical and perceived directions. Repulsion magnitude is measured as the size of the angle (θ).

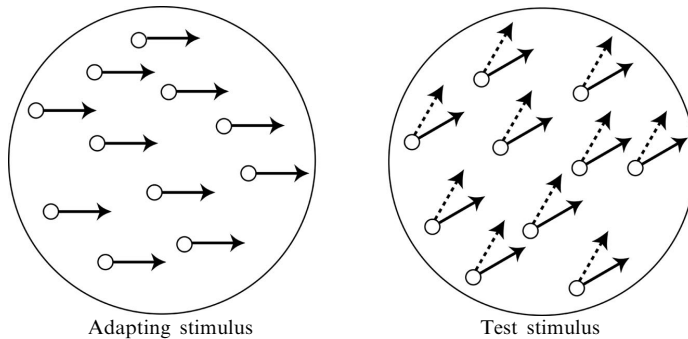


Figure 2. Schematic diagram of the direction aftereffect (DAE), showing the adapting stimulus (left) translating rightward (90°) and the test stimulus (right) translating at 60° clockwise of upward vertical (0°), as indicated by the solid arrows. Dotted arrows represent perceived direction, which is shifted angularly away from the adapting direction.

direction, and is invoked through the successive presentation of two unidirectional RDKs (adaptor and test) (figure 2). Thus, the DI and DAE are the results of, respectively, spatial and temporal contextual effects.

For the visual context, spatial or temporal, to influence motion perception, some level of integration of the visual scene must be taking place. Two stages of the human visual motion system hierarchy that have been implicated in motion integration are the primary visual cortex (V1) and the middle temporal area (MT). It is broadly accepted that V1 is responsible for extracting fine-grained local motion signals, first in layer 4C α , then layer 4B, which then feed into MT (Anderson et al 1998) where they are integrated to form a more global representation (Huk and Heeger 2002; Movshon and Newsome 1996; Qian et al 1994; Snowden et al 1991).

Investigations into the possible neural substrates of the DI and the DAE have yielded contradictory results. Some research has indicated that the DI may result from local motion processing early in the hierarchical motion pathway, ie in area V1 (Grunewald 2004; Hiris and Blake 1996; Marshak and Sekuler 1979; Wiese and Wenderoth 2007, 2010), while other studies attribute the DI to global motion processing in MT (Benton and Curran 2003; Curran et al 2009; Wilson and Kim 1994). Similarly, while some studies have suggested that the DAE results from the adaptation of early, local motion processes in V1 (Curran et al 2006, 2009), others have produced evidence that the DAE arises later from the adaptation of global motion processes in MT (Patterson and Becker 1996; Schrater and Simoncelli 1998; Wiese and Wenderoth 2007, 2010).

Evidence that the DI arises from local V1 processing comes from dichoptic studies, in which the inducer is presented to one eye and the test to the contralateral eye. These studies have shown that, under such circumstances, the size of the shift in the perceived test direction is reduced to $\sim 60\%$ of the value observed with binocular or monocular presentation (Grunewald 2004; Marshak and Sekuler 1979; Wiese and Wenderoth 2007, 2010). Because all cells in MT respond to binocular stimulation to a greater or lesser extent, ie stimulation in either eye (Maunsell and van Essen 1983) while many V1 cells (in layer 4C α) respond only to monocular input (Merigan and Maunsell 1993; Poggio and Poggio 1984), the $\sim 60\%$ interocular transfer (IOT) suggests a V1 locus for DI-associated motion processing.⁽¹⁾ In agreement with this, Hiris and

⁽¹⁾These results have been contested (Curran et al 2009) on the basis that the DI is also reduced during binocular rivalry (Chen et al 2005). Binocular rivalry is the involuntary alternation between two percepts when dissimilar images are presented dichoptically. However, Wiese and Wenderoth (2010) have recently shown that the IOT of the DI is reduced when induced with a centre-surround dichoptic display, which prevents binocular rivalry.

Blake (1996) reported that DI magnitudes remain unchanged whether the two dot sets are presented at different disparities or are coplanar. This has been interpreted as evidence that the substrate of the DI is found early in the motion-processing pathway (Grunewald 2004; Wiese and Wenderoth 2007). Since binocular disparity-tuned cells are found in MT (Maunsell and van Essen 1983) and in layer 4B of V1 (DeYoe and Van Essen 1985; Hubel and Livingstone 1987; Poggio and Poggio 1984), the evidence suggests an even earlier processing stage, such as layer 4C α .

Contrary to the evidence that the DI is driven by early local processing in V1, Benton and Curran (2003) have shown that the DI arises from global processing in MT. They first measured the DI in a bidirectional RDK across several inducer speeds. They also measured the DI invoked by a display consisting of a set of dots all moving at the average of these inducer speeds. They then measured the DI with a mixed-speed inducer, which consisted of all of these speeds, and therefore contained both local and global motion signals, the local signals being those of the component speeds and the global signal being the average speed. They reasoned that, if the DI arises from local motion processing, then the size of the DI invoked by the mixed-speed inducer should correspond with the vector average of the DIs invoked by the individual speeds; but if the DI arises instead from global motion processing, then the size of the DI invoked by the mixed-speed inducer should correspond to the DI invoked by the set of dots moving at the average speed. They found the latter to be the case. Patterson and Becker (1996) have shown that the DI can be invoked in a cyclopean display, in which the drifting dots are defined purely by binocular disparity and are not monocularly visible. Since binocular disparity-tuned cells are only found beyond layer 4C α of V1 (see Born and Bradley 2005), this implies that the neural substrate of the DI also lies beyond this stage, possibly in MT.

The DAE, like the DI, has been attributed by some to early local motion processing in V1 and by others to later global motion processing in MT. Curran et al (2006) have provided evidence that the DAE stems from local motion processing, indicating an early V1 substrate. Using a mixed-speed stimulus, similar to that with which they tested the DI, but this time as an adaptor, they showed that the size of the DAE is determined by the adaptor's local component speeds and not by its global average speed. Curran et al (2006) produced further evidence that the DAE is driven by local V1 adaptation by showing that the size of the shift in the perceived test direction is reduced to $\sim 70\%$ when the DAE adaptor is presented to the eye contralateral to the test stimulus.

Contradicting Curran et al's (2006) results, Wiese and Wenderoth (2007) found the DAE to exhibit 100% IOT, indicating that it arises from binocular processing at least beyond layer 4C α of V1, possibly in MT. Also in support of an MT locus of the DAE, Patterson and Becker (1996) found, as they did with the DI, that the DAE could be invoked in a cyclopean display where no monocular figures are visible. In a second experiment, they also found that a cyclopean adaptor could invoke a DAE in a luminance-defined test stimulus, and vice versa. Because the DAE transfers across stereoscopic and luminance domains, their substrates must overlap substantially, suggesting that each of these effects is mediated by higher cortical areas involving substantial binocular processing, such as MT. Further evidence that the DAE arises from global motion processing in MT comes from Schrater and Simoncelli (1998). In one experiment, they measured the DAE using a grating stimulus as the adaptor and a plaid (two superimposed component gratings with different orientations) as the test. While isolated gratings present only local "component" motion signals that are processed in V1, the global motion percept of plaid direction is signalled by "pattern" cells in MT (Movshon et al 1985). The test stimulus was configured in such a way that its perceived direction would be shifted towards or away from the adaptor depending on

whether the DAE was operating at the local or global stage. They found the latter to be true.

Curran et al (2009) conducted a study to test for evidence that the DI and DAE arise from different motion processing stages and to investigate where in the motion processing pathway these stages might lie. To this end, they set out to establish whether there is a sequential order in which the two phenomena arise and, if so, what that order is. Curran et al (2009) (experiment 1) used a bidirectional mixed-speed RDK adaptor, wherein fast and slow (7 and 2 deg s^{-1}) motion components moved in directions 25° either side of vertical. They subsequently measured the DAE with a unidirectional (vertical) mixed-speed (fast and slow) RDK test. They showed that the fast motion component of the test was directionally shifted away from the fast adaptor component and the slow test component was directionally shifted away from the slow adaptor component, resulting in the unidirectional test RDK being perceived as bidirectional. Further, they found that the magnitude of the perceived separation of the test stimulus components was not consistent with the DAE alone, but could be accounted for by the presence of a DI also arising within the perceptually bidirectional test stimulus. Note that the DAE could not have arisen after the DI, since without the DAE the test stimulus would have remained unidirectional. The results suggest that the DI does not arise from an earlier stage of processing than the DAE. In the same experiment, Curran et al (2009) measured the DAE in both a 2 deg s^{-1} and a 7 deg s^{-1} single-speed test to obtain an estimate of the bidirectional DAE without the 'subsequent' DI also occurring. They then measured the DI with test and inducer directions determined by the obtained single-speed DAE values. They found that the combined bidirectional DAE and DI was of the same size as the separate DAE and DI shifts combined in a simple linear addition.

In a second experiment, Curran et al combined DI- and DAE-invoking stimuli in such a way that the perceived test direction would be shifted either away from or towards the adapting direction, depending on the order in which the two processes occur in the visual system (figure 3). Participants adapted to a bidirectional RDK that invoked a DI. They were then presented with a unidirectional RDK test with a direction midway between one of the actual adapting directions (a1) and its DI-induced perceived adapting direction (p1). The resulting DAE was a shift away from the actual adapting direction rather than from the perceived adapting direction, implying adaptation to the actual adaptor directions and not to the perceived adaptor directions. Curran et al (2009) concluded that DAE-invoking adaptation was occurring at a processing stage that preceded DI-invoking processes, and that this in turn, when combined with the evidence that the DAE arises from local motion processing and the DI from global motion processing (Benton and Curran 2003; Curran et al 2006), implies that the neural substrate of the DAE is located within V1 while the DI is driven by processes within MT.

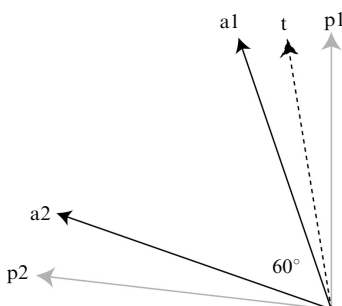


Figure 3. Vector diagram from Curran et al (2009) showing actual adaptor directions (a1 and a2), separated by 60° , perceived adaptor directions (p1 and p2), and the test direction (t), which was midway between the nearest actual (a1) and perceived (p1) directions.

The accumulated evidence from the investigations into the neural loci of the DI and DAE outlined above is thus inconclusive. Importantly, however, the majority of studies that have investigated and compared these phenomena within the same paradigm (eg Benton and Curran 2003; Curran et al 2006, 2009; Wiese and Wenderoth 2007) indicate that they do at least exhibit different characteristics and are therefore likely to arise from largely separate processing sites.

Adopting a similar strategy to that of Curran et al’s (2009) experiment 2, but employing different stimuli, in the current study we sought to compare the tenability of two models, one contending that the neural activity underlying the DI occurs prior to that underlying the DAE (DI-first model) (figure 4a) and the other that the neural processes underlying the DAE operate prior to those underlying the DI (DAE-first model) (figure 4b). Implicit to both models is that the outputs of the two processing stages combine additively, as reported by Curran et al (2009). In the strictly sequential models tested here, where all processing relevant to the effect (DI or DAE) in stage 1 is entirely complete prior to any processing leading to the effect in stage 2, this is the only logical possibility. Our objective, therefore, was to attempt to discount the possibility either that DI-related processing precedes DAE-related processing in a linearly additive fashion or that DAE-related processing precedes DI-related processing in a linearly additive fashion.⁽²⁾ We approached our objective by measuring the DI and DAE in combination, ie as they are experienced simultaneously. We also measured the two phenomena separately in the two possible sequential orders that their processing could be occurring. To test the DI-first model, we measured the DI followed by the DAE, and to test the DAE-first model, we measured the DAE followed by the DI. For each, the test stimulus direction used in the second measurement was determined by the value obtained in the first measurement. We thus ‘manually’ combined the outputs of the DI- and DAE-invoking processing stages sequentially to obtain predictions that could be compared to the outcome of the two phenomena arising in combination. We reasoned that, if there is a particular sequential order to the processes underlying the two phenomena, then one of our sequential measurements should produce a result that is similar to that obtained when the two are invoked in combination.

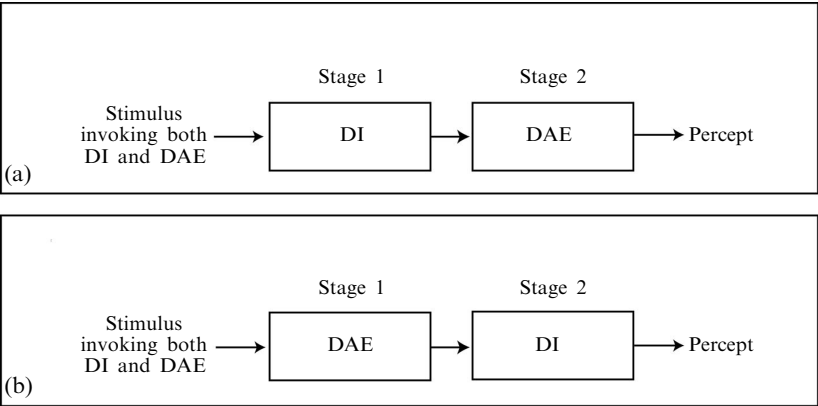


Figure 4. The DI-first and the DAE-first models. A stimulus that invokes both a DI and a DAE generates a percept that represents the resultant of the summing of the outputs of two stages of processing. (a) In the DI-first model, the neural processes responsible for the DI (labelled ‘DI’, in the interests of brevity) operate at stage 1 and those responsible for the DAE (labelled ‘DAE’) operate at stage 2. (b) The DAE-first model dictates that DAE-generating activity occurs first, at stage 1, and that DI-producing activity occurs at stage 2.

⁽²⁾ Hereafter, the term ‘sequential’ will also imply linear additivity.

2 Experiment 1

The first experiment was designed to measure the DI and DAE individually, as well as the effect of the DI and DAE operating in combination. We labelled the 3 respective conditions DI₁, DAE₁, and Combined (figure 5).








Condition	Stimulus configuration	
	adaptation	test
DAE ₁	adaptor −90° 	test 0°  Perceived
DI ₁	no adaptation	test 0°  inducer 90°  Perceived
Combined	adaptor −90° 	test 0°  inducer 90°  Perceived

Figure 5. Stimulus conditions in experiment 1. In the DAE₁ and Combined conditions, the 0° test stimulus was preceded by a −90° (90°) adaptor. In the DI₁ and Combined conditions, the test stimulus and 90° (−90°) inducer were presented simultaneously. While the actual experiment was counterbalanced with an equal number of CW- and CCW-oriented displays, shown here are the CW-oriented displays only, in which the DAE adaptor is at −90° and the DI inducer is at 90°.

2.1 Method

2.1.1 Apparatus. All stimuli were generated and all responses recorded with Vpixx v2.3 (VPixx Technologies, Longueuil, Canada, www.vpixx.com). The software was run on a G5 Macintosh Dual 2 GHz Power PC running Mac OS X version 10.4.11. The SONY Trinitron Multiscan G520 monitor had a frame refresh rate of 75 Hz and a pixel resolution of 1152 × 870 pixels. Participants viewed the screen binocularly from a distance of 57 cm through a cylinder (diameter 33 cm, length 57 cm) that was lined internally with matte-black felt, and a chin-and-head-rest prevented head movement.

2.1.2 Stimuli. Stimuli consisted of either a unidirectional or bidirectional white-on-black RDK (dot diameter 0.08 deg, lifetime 0.7 s, density 4 dots deg^{−2} for each direction) within a circular aperture subtending 8 deg, which was centred on a red fixation point (diameter 0.15 deg) in the middle of the screen. Each set of dots translated coherently in a given direction at 2.5 deg s^{−1}.

The DI inducing stimulus and the DAE adapting stimulus drifted horizontally either leftward (−90°) or rightward (90°), with positive values indicating directions CW of upward vertical. The test stimulus drifted vertically upward (0°). Combining the two stimuli to measure the combined effect of the DI and DAE involved the presentation of the −90° DAE adaptor followed by the presentation of the 0° test together with the 90° DI inducer (see figure 5).

In the DAE₁ and Combined conditions, the initial adaptation period was 60 s, followed by a 500 ms interstimulus grey mask and a tone to signal the beginning of the block of test trials. Trials were interspersed with 5 s top-up adaptation periods. The test stimulus was presented for 0.7 s. In the DI₁ conditions, the test and inducing stimuli were presented simultaneously for 0.7 s. In all conditions, at the offset of the stimulus a pointer appeared, occupying the same central aperture.

2.1.3 Participants. Eight participants, four male and four female, were tested. Five were psychology students at Macquarie University, one was a staff member, and two were not affiliated with the university. Two of the participants were aware of the aims of the study. All were emmetropic or had corrected-to-normal vision.

2.1.4 Procedure. Instructions, a demonstration, and a block of practice trials preceded testing. For each trial, participants were required to judge the direction of the test stimulus. For DI conditions, participants were instructed as to which set of dots they were to judge. Participants responded to a subsequently presented pointer, which was initially set at either $\pm 15^\circ$ of the vertical RDK drift direction. Left and right arrow key presses resulted in the orientation of the pointer being shifted in the subsequent trial either CCW or CW, as determined by an adaptive staircase routine.

A fully randomised interleaved double staircase was used, and measurements were counterbalanced with an equal number of trials conducted with a CW-oriented display (as depicted in figure 5) and CCW-oriented display. The CCW display reflected the CW display about the vertical axis. CW and CCW trials were conducted in separate blocks, and values were later combined for graphical representation and are reported as a single value measured in degrees CW of upward vertical, as if all conditions were CW. Since CW and CCW measurements were counterbalanced, no baseline adjustment was necessary. Step sizes for each reversal were 8° , 6° , 4° , 2° , and 1° thereafter. Each condition was terminated after 10 reversals or a maximum of 30 trials, with the mean of the final 6 reversals from each staircase averaged to give the estimated perceived direction.

2.2 Results and discussion

Results from experiment 1 are presented in figure 6. We obtained a mean DAE of 7.25° , a mean DI of -14.42° , and a mean combined effect of -2.52° . One-sample two-tailed *t*-tests showed a significant difference from zero for each of the DAE₁ ($t_7 = 4.51$, $p = 0.003$, $\eta^2 = 0.744$) and DI₁ ($t_7 = -4.66$, $p = 0.002$, $\eta^2 = 0.756$) conditions.

That the DI₁ condition produced a significant effect was expected since the DI occurs up to and beyond inducer-test directional differences of 90° (Dakin and Mareschal 2000). The DAE₁ condition also yielded a significant, though smaller, effect. This finding is in general agreement with previous DAE measurements with adaptor-test directional differences of 90° (Patterson and Becker 1996; Schrater and Simoncelli 1998; Wiese and

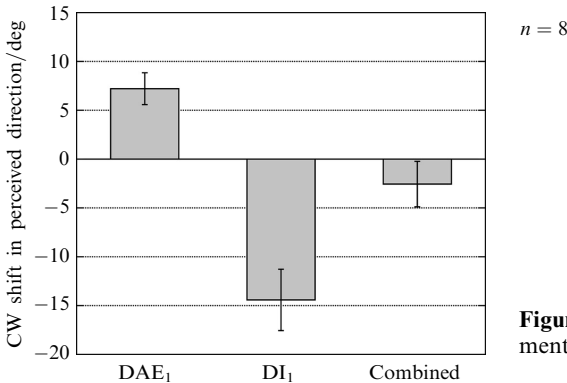


Figure 6. Graph showing the results of experiment 1. Error bars represent ± 1 SE.

Wenderoth 2007). It should be noted that the value obtained in the Combined condition is not comparable to a sum of the DI_1 and DAE_1 values, since the two phenomena have not been measured in sequence. Measuring the final outcome of the two processing stages in sequence involves first measuring the directional shift due to the first phenomenon and then using the obtained value as the initial direction of the test stimulus in the configuration used to invoke the second phenomenon. Thus, in experiment 2, the direction of the test stimulus in each condition was determined by the shift measurement obtained in the appropriate condition in experiment 1.

3 Experiment 2

In experiment 1, we obtained measurements DAE_1 and DI_1 for the respective effects when using a vertical test stimulus. In experiment 2, we manually combined the output of DI -related processes (DI_2 condition) with the prior output of DAE -invoking processes (DAE_1), and we manually combined the output of DAE -generating processes (DAE_2 condition) with the prior output of DI -invoking processes (DI_1) to obtain respective predictions based on the DAE -first and DI -first models for the Combined condition data from experiment 1. To this end, in the DAE_2 condition, the test direction for each participant was set to the respective perceived test direction obtained from the DI_1 condition, and in the DI_2 condition the test direction for each participant was set to the respective perceived test direction obtained from DAE_1 (figure 7). The predictions that would be made by the DAE -first model can therefore be expressed as the sum, $DAE_1 + DI_2$, and the DI -first model as $DI_1 + DAE_2$.




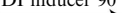
Condition	Stimulus configuration	
	adaptation	test
DAE_2	<div>DAE adaptor -90° </div>	<div>test DI_1° </div>
DI_2	<div>no adaptation</div>	<div>test DAE_1°  DI inducer 90° </div>

Figure 7. Stimulus conditions in experiment 2. DI_2 -inducing direction = 90° (-90°), and test direction = DAE_1 value; DAE_2 -adapting direction = -90° (90°), and test direction = DI_1 value. While the actual experiment was counterbalanced with an equal number of CW and CCW-oriented displays, only CW-oriented displays are shown here, in which the DAE adaptor is at -90° and the DI inducer is at 90° .

3.1 Method

The participants, apparatus, and stimuli in experiment 2 were identical to those in experiment 1, with two exceptions: the test stimulus directions were determined by DAE_1 and DI_1 measurements for each individual and for each direction (CW and CCW) in experiment 1, and the Combined condition was omitted. As with experiment 1, CW and CCW results were later combined for graphical representation.

3.2 Results and discussion

The results from experiment 2 are shown in figure 8. The DAE₂ and DI₂ conditions yielded respective shifts of 7.48° and −14.47°. One-sample two-tailed *t*-tests showed significant effects for the DAE₂ (*t*₇ = 3.30, *p* = 0.013, η^2 = 0.609), and DI₂ (*t*₇ = −6.27, *p* < 0.0005, η^2 = 0.849) conditions.

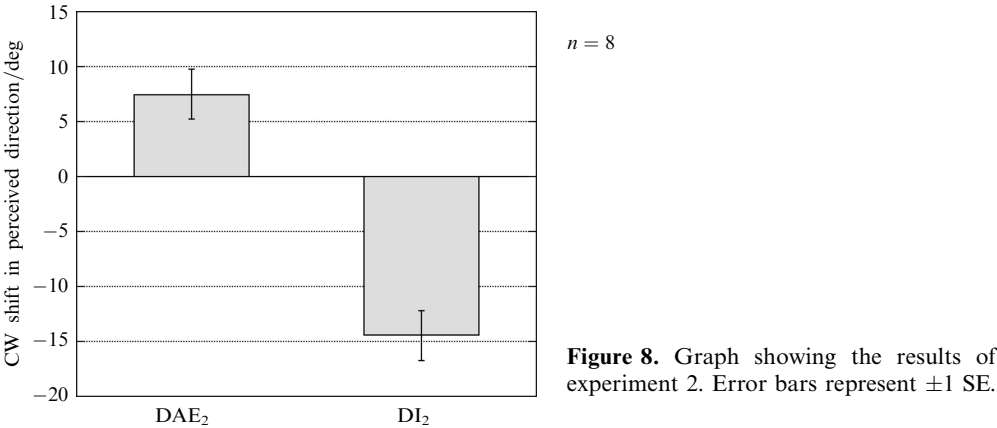


Figure 8. Graph showing the results of experiment 2. Error bars represent ±1 SE.

Figure 9 shows the final predictions of the DAE-first and DI-first models, and the Combined result from experiment 1. The final result of the DAE-first model is given by the sum DAE₁ + DI₂, and the final result of the DI-first model is given by the sum DI₁ + DAE₂. It should be emphasised that the calculations were made with values obtained for each individual. Having obtained measurements of the DI and DAE in the two possible sequential orders in which their respective underlying processes may occur, we were able to compare each prediction to that obtained with the two phenomena being invoked in combination. Paired two-tailed *t*-tests showed a significant difference between DAE₁ + DI₂ and Combined (*t*₇ = 3.359, *p* = 0.012, η^2 = 0.617) but no significant difference between DI₁ + DAE₂ and Combined (*t*₇ = 1.405, *p* = 0.203, η^2 = 0.220) (critical α was Bonferroni-adjusted to control the experiment-wise error rate).

Hence, we found that the prediction made by measuring the DAE followed by the corresponding DI (DAE-first model) was dissimilar from the result of the two measured in combination. The additive DAE-first model can therefore be rejected, and we may conclude that DAE-invoking neural activity does not arise sequentially earlier than DI-invoking processes. On the other hand, we found that the prediction made by

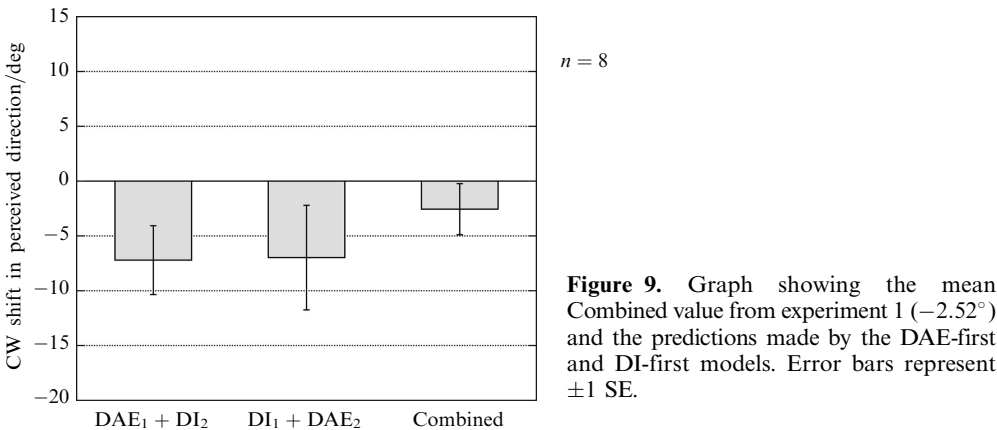


Figure 9. Graph showing the mean Combined value from experiment 1 (−2.52°) and the predictions made by the DAE-first and DI-first models. Error bars represent ±1 SE.

measuring the DI followed by the corresponding DAE (DI-first model) was not dissimilar to that of the two measured in combination, and hence we cannot discount the additive model in which the DI arises from sequentially earlier processing than that of the DAE.

4 General discussion

The current experiments employed a two-stage process analogous to the possible sequential neural processing underlying the DI and the DAE. Manually parsing the combined effect of the DI and DAE into its two constituents by measuring the two phenomena individually in both possible sequential orders in which their underlying processes may occur allowed us to test the tenability of two models: the DAE-first model and the DI-first model. Having found that the DAE-first prediction was dissimilar from the result obtained when the phenomena were combined, but that the DI-first prediction was not, we have rejected the DAE-first model but failed to reject the DI-first model. We may conclude from these results that the effect of the DI and DAE operating in combination is not the result of DAE-invoking activity occurring at a sequentially earlier stage of motion processing than DI-invoking activity. A distinction should be made here for the sake of clarity. The finding that the DAE does not arise from sequentially earlier processing than the DI does not necessarily imply that the DI arises from sequentially earlier processing than the DAE. In fact, we cannot assume that the combined effect is necessarily the result of the DI arising from a sequentially earlier stage of motion processing than the DAE, since we must also consider the possibility that the two phenomena combine non-sequentially.

4.1 *Conflict and consonance with earlier findings*

Our results are substantially consistent with many of the studies reviewed in the introduction. However, given the fact that this body of literature already presents contradictory findings, it is inevitable that our results must conflict with at least some. If we consider the possibility that the DI arises from an earlier processing stage than the DAE, then in the tradition of the antecedent literature, we might infer that the DI is likely to arise from local motion processing within V1 and that the DAE is likely to arise from global motion processing in MT. Many of the studies described in the introduction have produced results that are consistent with this conclusion, notably those that attribute the DI to processing in V1 (Grunewald 2004; Hiris and Blake 1996; Marshak and Sekuler 1979; Wiese and Wenderoth 2007, 2010), and those that attribute the DAE to the adaptation of MT cells (Patterson and Becker 1996; Schrater and Simoncelli 1998; Wiese and Wenderoth 2007, 2010). However, as we have seen, there is also evidence that places the respective neural substrates of the DI and the DAE in MT and in V1, respectively (Benton and Curran 2003; Curran et al 2006, 2009; Wilson and Kim 1994). Of particular relevance to the current study are the findings of Curran et al (2009) who, like us, have investigated the possible sequential order of the processes underlying the DI and DAE. In their first experiment, Curran et al found that the DAE does not arise from a later stage than the DI. Rather than assuming at that point that DAE-related activity must therefore sequentially precede that of the DI, they acknowledged that the two phenomena may result from non-sequential “iterative processing occurring within a single neuronal population” (Curran et al 2009) within the motion processing hierarchy. As described in our introduction, the DAE observed in their second experiment corresponded to adaptation to the actual adaptor directions and not to the perceived adaptor directions, and from this they made the further, more definitive claim that DAE-related processing does in fact occur sequentially earlier than DI-related processing. Since our data indicate that the DAE does not arise from sequentially earlier processing than the DI, we must attempt to reconcile our own finding with that of Curran et al (2009).

4.2 *Reconciliation of findings*

One way to reconcile Curran et al's (2009) results with our own is to attribute the discrepancy to differences in the stimuli employed. Curran et al used bidirectional RDK-adapting stimuli, which thereby differed from ours, and from those used traditionally in DAE studies. Our own stimulus presents one potential confound, since the -90° DAE adaptor may perceptually alter the subsequently presented 90° DI inducer. Past investigations have found no DAE when the adaptor and test stimuli are separated by 180° (eg Levinson and Sekuler 1976), so the DAE adaptor should have had no directional effect on the DI inducer. However, other studies have produced results that suggest that the DAE adaptor may have affected the DI inducer's perceived speed. The velocity aftereffect (VAE) is the change in perceived speed of a test stimulus following adaptation to motion in the same or opposite direction. When the test direction is opposite that of a same-speed adaptor, its velocity has been found to increase slightly (Scott et al 1963), to be unaffected (Schrater and Simoncelli 1998), to be variably affected (Rapoport 1964), and to decrease slightly (Carlson 1962; Smith 1985; Thompson 1981). The possible occurrence of the VAE might be considered problematic, since the DI has been found to be speed-tuned, with the largest shifts in perceived direction occurring with inducer–test speed ratios of between 1:1 and 3:1 (Curran and Benton 2003; Dakin and Mareschal 2000; Lindsey 2001; Marshak and Sekuler 1979). However, the VAE studies mentioned above found the effect to be very small, and its impact on our data is likely to be negligible. There are also possible confounds introduced by a bidirectional DAE adaptor such as that employed by Curran et al (2009), since the influence of the second adapting direction is unknown. While it may possibly have confounded the findings of their first experiment, it is unlikely to have altered the findings of their second, since it differed from the test direction by $\sim 65^\circ$, at which point the DAE has been shown to be of negligible size (eg Wiese and Wenderoth 2007). Our results cannot therefore be reconciled with those of Curran et al by attributing the discrepant findings simply to differences in the display. Alternatively, there is a possibility that Curran et al's experiment 2 finding results from non-sequential processing. If the combined effect of the DI and DAE were arising through parallel channels, for example, then the processes invoking the DAE would be independent of those invoking the DI, and vice versa. In Curran et al's experiment, both phenomena would therefore have been invoked by the actual adaptor directions, producing the same result. Attributing the combined effect of the DI and the DAE to non-sequential processing therefore reconciles the findings of the current study with those of Curran et al (2009).

4.3 *Multilevel processing*

In line with this suggestion, discrepancies throughout the literature have led some authors (eg Wiese and Wenderoth 2010) to propose that the DI and the DAE each arise from activity at multiple processing stages. As described in the introduction, both phenomena have been found to exhibit characteristics of both local and global processing in different situations. With the exception of one directly contradictory finding, that the DAE shows both 100% IOT (Wiese and Wenderoth 2007) and $\sim 70\%$ IOT (Curran et al 2006), the apparent disagreement in the DI and DAE literature is resolved once the phenomena are attributed to multilevel processes. If it is the case that both V1 and MT processing are involved in generating both the DI and the DAE, this would preclude the possibility that the two phenomena arise from sequential processing.

4.4 *Recurrent processing*

A further complicating factor is the well-documented involvement of recurrent processing, the feedback of signals from higher to lower processing stages, in the visual integration hierarchy (see Lamme and Roelfsema 2000). Feedback signals from MT to V1 have been shown to contribute to the perception of coherent motion stimuli (Harrison et al 2007).

Since the DAE is invoked by the presentation of coherent unidirectional motion, it is likely to arise from adaptation of cells involved in such feedback loops. The DI is invoked by a bidirectional stimulus, with its two components moving relative to one another. From recordings of single- and multi-cell responses in macaque V1, the inactivation of MT has been shown to decrease V1 responses to relative motion (Hupe et al 1998). There is thus a further possible role for recurrent processing in the occurrence of the DI. Using transcranial magnetic stimulation (TMS), Silvanto et al (2005) have found that V1 activity associated with the perceptual awareness of motion occurs both prior to and following MT activation. The involvement of multilevel, recurrent processing would not only preclude the possibility that the DI and DAE combine sequentially; it would also confound any correspondence between the temporal and structural hierarchies within the motion processing pathway. Thus, even if the DI and DAE were due to sequentially independent processing, by establishing the sequential order in which they arise we would not be able to infer the hierarchical order of their substrates. Multilevel recurrent processing may offer a very plausible reconciliation of the seemingly contradictory findings throughout the DI and DAE literature. Such processes would be likely to introduce substantial nonlinearities in the combination of the DI and DAE effects that might be revealed by further testing using a larger range of stimulus parameters than were employed in this study. However, formulating a model that reflects the complexities that such processing introduces is beyond the scope of the current paper.

4.5 Conclusion

We have shown that the DAE does not arise from neural activity at a sequentially earlier processing stage than DI-related activity. This has not been previously demonstrated. Our finding is an important one, particularly in light of Curran et al's (2009) finding that DI-related processing does not occur sequentially prior to that of the DAE. Together our studies cast doubt on the likelihood that the two phenomena arise from sequentially independent processing and, thereby, lend credence to a multi-level processing model. The conclusion that the DI and DAE are likely to arise from non-sequential neural processing stages takes into consideration the complexities introduced by recurrent, multilevel processing and resolves much of the disagreement in the literature regarding the processing stages that underlie the two phenomena.

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Appendix B

Ethics approval letter



15 December 2008

Professor Peter Wenderoth
Department of Psychology
Division of Linguistics and Psychology

Reference: HE27FEB2009-R06267

Dear Professor Wenderoth

FINAL APPROVAL

Title of project: "Psychophysical studies of visual perception" ✓

Thank you for your recent correspondence. Your response has addressed the issues raised by the Committee and you may now proceed with your research.

Please note the following standard requirements of approval:

1. Approval will be for a period of twelve (12) months. At the end of this period, if the project has been completed, abandoned, discontinued or not commenced for any reason, you are required to submit a Final Report on the project. If you complete the work earlier than you had planned you must submit a Final Report as soon as the work is completed. The Final Report is available at: http://www.research.mq.edu.au/researchers/ethics/human_ethics/forms
2. However, at the end of the 12 month period if the project is still current you should instead submit an application for renewal of the approval if the project has run for less than five (5) years. This form is available at http://www.research.mq.edu.au/researchers/ethics/human_ethics/forms. If the project has run for more than five (5) years you cannot renew approval for the project. You will need to complete and submit a Final Report (see Point 1 above) and submit a new application for the project. (The five year limit on renewal of approvals allows the Committee to fully re-review research in an environment where legislation, guidelines and requirements are continually changing, for example, new child protection and privacy laws).
3. Please remember the Committee must be notified of any alteration to the project.
4. You must notify the Committee immediately in the event of any adverse effects on participants or of any unforeseen events that might affect continued ethical acceptability of the project.
5. At all times you are responsible for the ethical conduct of your research in accordance with the guidelines established by the University
http://www.research.mq.edu.au/researchers/ethics/human_ethics/policy

If you will be applying for or have applied for internal or external funding for the above project **it is your responsibility** to provide Macquarie University's Research Grants Officer with a copy of this letter as soon as possible. The Research Grants Officer will not inform external funding agencies that you have final approval for your project and funds will not be released until the Research Grants Officer has received a copy of this final approval letter.

ETHICS REVIEW COMMITTEE (HUMAN RESEARCH)
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http://www.research.mq.edu.au/researchers/ethics/human_ethics

Yours sincerely

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