The many forms of motion processing:
How shape information affects motion recovery

Matthew F. Tang
B.A., B.Sc. (Hons.)
School of Psychology

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Abstract

Dominant models of visual processing commonly argue that shape and motion information generated by a moving object are separately processed in discrete, hierarchal neural pathways. There is now, however, a growing body of evidence showing that these two processes actually interact at a seemingly early stage of visual processing, contrary to the existing models. The central aim of the thesis is to examine the interaction of form information with three fundamental tasks of motion processing of increasing complexity; motion detection, direction processing and global motion integration. The thesis adds to this growing body of research and provides a novel model showing how and where in the visual system these interactions may occur.

The first study (Chapter 2) examined how form information alone can cause the perception of motion. This was done using the transformational apparent motion stimulus, where a shape change elicits the perception of motion in the direction explaining the change. The perceived motion direction is not predicted by motion energy models and instead shows that form information alone can cause motion to be detected. The study showed many transformational apparent motion stimuli can be globally integrated into a single, global percept, suggesting that the form information that causes the percept can enter the motion system by, at least, the stage of global motion pooling.

The second study (Chapter 3) examined an influential form-motion model that provides a potential mechanism for form information to influence motion processing. The model existing argues that the orientation cues generated by the extended integration time of V1 neurons (known as motion streaks) are multiplicatively combined in the same stage with a binary motion direction estimate. When this model was tested using visual aftereffects the orientation dependence of the aftereffect suggested that these form cues influence motion direction processing at a later stage of
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the processing hierarchy than predicted. A new model was developed that successfully accounted for the data where orientation-selective neurons in V1 modulate the gain of motion-selective neurons at a later stage of global motion integration.

The next two studies provide support for different aspects of the proposed model. A prediction from the model was first confirmed by showing that orientation information directly affects the stage of global motion integration (Chapter 4). Adapting to an oriented grating changed the perceived direction of a motion stimulus that was designed to null effects at the local motion level and with aftereffects instead most likely reflecting changes at the stage of global motion integration. The orientation and spatial frequency dependence of this aftereffect was also predicted by the model. The next study (Chapter 5) showed that the model predicts many instances where the orientation information associated with an object has been found to change its perceived direction. The result suggests that the shape of an object will modulate the gain of global motion selective neurons. These studies showed that orientation information most likely directly influences motion direction processing in the manner specified by the model.

The final study (Chapter 6) built upon the thesis’s key finding that form information enters the motion system by, at least, the stage of global motion integration. A well-known stimulus was used where an object translates behind opaque apertures, which has previously been claimed to show that form information can influence global motion integration. The study found little evidence that form information affected motion pooling. Instead, contrary to previous claims, integration was mainly determined by the representation of local motion information. The result did support a previous finding showing that shapes forming open contours are unlikely to be globally integrated, suggesting that some types of form information may act as segmentation cue.
Overall, the research presented in this thesis provides strong evidence that form information can influence motion processing and shows that this interaction likely occurs at the stage of global motion pooling. Furthermore a novel mechanism is provided that allows form information to directly influence motion processing.
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Statement of candidate’s contributions

The research presented in this thesis was designed and written by myself in collaboration with my primary supervisor, David Badcock and Edwin Dickinson. Mark Edwards contributed to the design and writing of Chapters 2 and 6. Edwin programmed the model used in the Chapters 3-5. My secondary supervisor, Troy Visser, also contributed to the writing of most of the chapters. I implemented all the programming for the experimental procedures, collected and analyzed the data. The co-authors of the manuscripts have individually approved these pieces of work for inclusion in this thesis.
Publications arising from this thesis


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A note about the demonstration movies

The movies referenced in this thesis can be downloaded from

https://sites.google.com/site/tangthesisdemos/. The movies for each chapter are
organized in separate folders and can be played in VLC or QuickTime. Optimal
demonstrations would often result from looping the shorter movies.
1 Introduction

The task of tracking a moving object in naturalistic visual scenes is highly complex. The visual system must first extract each object’s shape and texture to individuate the separate objects from each other and the background. Each of these signals then must be assigned to the same object as it moves through space but not those signals generated by other objects and one’s own movement through the environment. This task involves segmenting moving shapes from the background and integrating motion information over time. If these objects rotate relative to the observer then the retinal image will change, but will still need to be assigned to the same object. The visual system must, therefore, be able to process shape changes while simultaneously tracking a moving object. This task becomes increasingly computationally complex with the hierarchal processing of sensory information, as simple inputs are transformed into the rich and textured objects of conscious experience.

The perceptual system uses parallel processing to neurally encode the information required for these tasks, with separate cortical streams processing different sensory modalities, and different subsets of information being further separately processed within each modality. The best-described distinction in visual processing is
that between form and motion information, with neurophysiological evidence showing that different visual neural pathways process these two types of information, with one type of visual information still being available after the other neural pathway has been ablated (Braddick et al., 2000; Livingstone and Hubel, 1987; Mishkin et al., 1983; Ungerleider and Haxby, 1994). For example, patients with lesions to a motion processing area (V5) perceive the world as a series of static images (Zeki, 1991), whereas those with lesions to form-processing areas are less able to recognize objects while still showing normal motion discrimination performance (Culham et al., 2003; Gallant, Shoup, & Mazer, 2000; Milner and Goodale, 1995).

Psychophysical evidence, based on tasks showing that one type of visual processing is possible without the other information, often supports this distinction. For example, a field of small dots can convey a global motion percept without the field containing any global shape information, showing the motion can be conveyed without a reference to a specific shape (Williams and Sekuler, 1984). Furthermore, the perceived direction of apparent motion generally follows the luminance distribution, not the shape information (Anstis, 1980). Conversely, form perception can occur with rapid presentation time (40 ms) that would preclude eye movements from generating motion signals in otherwise static stimuli (VanRullen and Thorpe, 2001). This shows form perception is not dependent on motion information within the image in normal circumstances.

While these examples show that form and motion can be independently processed they do not show it necessarily has to be. This thesis will examine, and add to, the growing body of research showing that form and motion information can interact at the early or middle stages of visual processing; a finding that is unaccounted for by most existing models of visual perception.
1.1 The visual system

Before describing the research showing how form and motion information can interact, it is necessary to outline the conventional view of the visual system. Light reflected from an object in motion casts a moving image over the retina. Retinal ganglion cells (RGCs) fire in response to the luminance and texture changes associated with the image. Unlike the three-dimensional object causing the motion, the retinal image is two-dimensional (2D) and can be represented in x-y-t space (Figure 1, Adelson and Bergen, 1985). This representation allows motion to be considered in frequency (f-x-y-t) space and allows for a simple estimation of the object’s speed and direction based on the orientation and length of the representation.

Figure 1. An example of how displaying motion stimuli in x-y-t space allows direction to be derived from orientation. a. A bar moving to the right. The motion in depicted in x-t for simplicity because there is no movement in this case in y space meaning the dimension can be omitted. b-d. The same rightward-moving bar depicted in x-t space with different sampling frequencies. This shows that the motion direction can be derived regardless of sampling frequency; and, thus, can account for apparent motion (AM).
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Separate processing of different types of visual information begins at the retina with the separation between cone and rod photoreceptors, which are specialized for detecting light with different spectra. Further separation occurs in the parvocellular and magnocellular pathways in the lateral geniculate nucleus (LGN). The vast majority (~80%) of RGCs are small Midget cells, projecting to the top four layers of the lateral geniculate nucleus (LGN), known as P cells that make up the parvocellular pathway (Kaplan, 2008). Larger M cells with receptive fields approximately 6-8 times larger than P cells (~10% of RGCs) project to the bottom two layers of the LGN, and make up the magnocellular pathway. The standard dichotomous view asserts that the parvocellular pathway is highly responsive to form information, but responds poorly to motion (Livingstone and Hubel, 1987; Pokorny, 2011; Pokorny and Smith, 1997), while the magnocellular pathway shows high temporal sensitivity, but responds poorly to contours and shapes (Ramachandran and Gregory, 1978). However, the extreme version of the dichotomy understates potential overlaps in sensitivity along the central stimulus dimensions (Kaplan, 2008).

The separation between magnocellular and parvocellular pathways is maintained in cortex. The magnocellular and parvocellular pathways project to different cortical layers in V1, with the different layers then mainly projecting separately to the dorsal and ventral pathways (McCool and Britten, 2008). From V1, the ventral stream projects through V2, V4, and temporal occipital cortex (Goodale and Milner, 1992; Milner and Goodale, 1995; Wilson and Wilkinson, 2015). The dorsal pathway, instead, sends information through V3a, MT/V5, MST, and V6 to parietal areas (Kourtzi et al., 2001; Movshon and Newsome, 1996; Pitzalis et al., 2010; Tootell et al., 1997). The ventral pathway appears highly specialized for recovering static form with area V4 responding strongly to shapes (Nandy et al., 2013; Pasupathy and Connor, 2001), and Fusiform
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Face Area to faces (Kanwisher and Yovel, 2006). The dorsal pathway appears crucial for extracting motion in the environment (Born and Bradley, 2005) and underlies grasping and reaching (Milner and Goodale, 1995), in addition to self-motion for locomotion purposes (Anderson and Siegel, 1999; Duffy and Wurtz, 1991a,b; Orban et al., 1992).

1.1.1 Local motion detection

Motion of the object is initially signaled by spatiotemporally-oriented V1 neurons that are selective for certain orientations and directions of motion, which respond to local regions of the visual field. The earliest motion detector was described in retina (Barlow and Levick, 1965) and V1 (Hubel and Wiesel, 1959) consisting of two spatially-separated neurons connected to a third ‘coincidence detector’. When a moving object triggers both primary neurons, at a certain temporal offset, the coincidence detector then signals a particular direction of motion. There is strong evidence for this model of motion detection in invertebrates but not in mammals (Behnia et al., 2014). Currently, the dominant conceptualization of motion detectors for mammals is based on the ‘motion energy’ model (Adelson and Bergen, 1985, see also Borst and Euler (2011) for a review).

In this model, motion is detected by a pair of non-directionally tuned spatial and temporal filters (Figure 2) configured as two quadrature paired filters that are half a cycle out of phase. This step gives the directional selectivity for motion direction. This output signal is rectified (either half or full wave (Solomon and Sperling, 1994)) and contrasted with an opposite direction signal. The overall output is termed motion energy.
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Figure 2. A schematic diagram of the motion energy detector proposed by Adelson and Bergen (1985).

The two spatial and temporal filters. Each filter has an odd (blue line) and even (red line) response.

Separable linear filters given by the combination of odd and even spatial and temporal filters. Only two of the four possible combinations are show for clarity. d-e, Spatiotemporal linear filters given by multiplying b and c. These are selective for leftwards (d) and rightwards (e) motion.

f. The two quadrature paired filters, the rectified and summed output of which gives the motion energy response.

There has been neurophysiological support for the motion-energy model with neurons in V1 having spatiotemporal receptive fields that are responsive to certain orientations across time, therefore giving direction and speed (DeAngelis et al., 1993). This model can also explain a number of motion illusions, such as reverse phi motion (Anstis and Rogers, 1986) and most apparent motion phenomena (Lu and Sperling, 1995). However, this is not the complete story. While motion energy detectors work on changes in luminance energy with time, the visual system can also detect the motion of
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objects defined only by contrast or texture changes with time through full-wave rectification of the changes after the initial stage of linear filtering (Badcock and Derrington, 1985; Cavanagh and Mather, 1989; Derrington and Badcock, 1985; Derrington et al., 1993, 1992; Edwards and Badcock, 1995, Wilson, Ferrera, Wilson, 1992). While motion energy detectors can derive the veridical motion direction from many classes of stimuli, they are limited by their physiological implementation. A single motion-selective neuron in V1 will only respond to a small part of a moving object because it has a small receptive field (~1° of visual angle (Cavanaugh et al., 2002; Hubel and Wiesel, 1968)). Because of the orientation selectivity of these neurons, they will only respond to components moving perpendicular to their preferred orientation. The motion energy response properties cause the neurons to produce directionally-ambiguous responses when an edge extends over the size of the receptive field. This is known as the ‘aperture problem’ (see Figure 3, Adelson and Movshon, 1982; Fennema and Thompson, 1979; Movshon et al., 1985).

Figure 3. An example of ambiguity introduced by the size receptive field size in V1, showing local motion signals are the same even though the global motion of the bars differs. The aperture represents a single neuron’s view of the stimuli. The red arrows indicate the direction the physical bar is moving and the yellow arrows indicate the local motion direction. The aperture problem means that all three receptive fields will perceive the same direction; perpendicular to the grating’s orientation which is not consistent with the bar’s motion direction.
1.1.2 Global motion integration

A moving object will cause many motion-selective neurons to produce motion signals that are individually directionally ambiguous, but when properly combined can signal the object’s true motion direction (known as global motion, see Figure 4). Additionally, when an observer moves through the environment the entire visual scene (including objects and background) will generate a set of motion signals which are consistent with the observer’s heading. There is strong psychophysical evidence that these global motion signals can be integrated over large areas (Burr et al., 1998). This provides a neurophysiological mechanism for multiple ambiguous signals, each subject to the aperture problem, to be integrated into a single coherent solution generally consistent with the object’s true direction. Three solutions have been proposed for how this might be achieved: intersection of constraints (IOC), vector averaging (VA), and feature tracking (FT) (Amano et al., 2009b; Edwards et al., 2012). All the solutions predict unambiguous 2D global motion from ambiguous 1D motion inputs with suitable stimuli. The IOC solution is based on the fact when a contour moves across an aperture, it produces an infinite number of possible motions in a 180° arc, all of which lie on a straight constraint line in 2D velocity space. The intersection of the constraint lines signals the global motion direction (Adelson and Bergen, 1985). Figure 4 illustrates how the IOC rule is implemented on a moving square, with a velocity-space representation shown in the left panel of Figure 5.
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**Figure 4.** A representation of a horizontally-moving square. The red circles represent the small receptive fields of neurons in V1, with the arrows showing a range of motion direction responses for that receptive field consistent with global horizontal motion. The solid black lines represent the constraint lines used in the IOC pooling solution. A velocity space representation of this stimulus is also shown in the left panel of Figure 5.

The grey arrows represent the velocity direction consistent with horizontal motion for each contour which is signaled by a single motion-selective neuron with a small receptive field (indicated by the red circle). The orientation and speed extracted from each local motion detector is referred to as the motion component. The constraint lines are perpendicular to the components and the point in space where these intersect represents the IOC solution to the aperture problem. In the case of the figure, the constraint lines intersect in the veridical direction of the square’s movement showing IOC can produce an accurate solution to the aperture problem (but see Yo and Wilson (1992) for failures of this integration strategy). IOC requires relatively complex computations, unlike VA, which gives the global motion direction simply by averaging motion components (Adelson and Movshon, 1982). VA has the added advantage of working well with non-rigid objects in motion (Badcock and Derrington, 1985; Derrington and Badcock, 1992). FT is the third solution that has received the least
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support, but it can be used when the motion-energy signature has been equalized (Alais, Wenderoth, and Burke, 1994; Alais Wenderoth, and Burke, 1997; Smith, 1994; Wenderoth, Alais, and Burke, van der Zwan, 1994). As the name suggests, the features of an object are tracked and matched as it moves through space but uniquely can have both top-down (i.e. attentional) and bottom-up inputs (Caplovitz and Tse, 2005, 2006; Lu and Sperling, 1995; Tse and Caplovitz, 2006). For example, the corners of the square could be the features that are tracked in Figure 4 to establish the trajectory of the moving square. This solution has the benefit of incorporating form information in motion processing. However, the relationship of FT with the rest of the motion system is currently poorly understood.

While in most cases IOC can accurately predict veridical motion, it has been shown to fail in other cases. Local motion pooling is most often studied using plaid motion, where two sinusoidal drifting gratings with different orientations and/or speeds are multiplied together. The two different motion signals can combine, producing a global motion solution not contained separately in either grating. For example, when two gratings, one with a 45° orientation and other with a 135° orientation, with identical speeds are superimposed they create a global motion with a 90° direction (see Figure 5). There are two types of motion integration, Type 1 and Type 2, within this velocity-space framework. Type 1 motion is when both IOC and VA solutions lie between the two one-dimensional components, while Type 2 is when the IOC prediction lies outside of these components (Wilson et al., 1992). In these patterns, if the components have different speeds then IOC and VA produce different solutions (Adelson andMovshon, 1982). The IOC and VA solutions appear to work simultaneously as adapting to motion in one solution direction shifts the perceived direction to the other solution (Bowns and Alais, 2006). A more recent study (Amano et al., 2009b), found that the visual system
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switches pooling solution depending on the local content of the motion information. The IOC rule is used when the local motion signals are ambiguous 1D signals but VA is used when these are 2D signals. This suggests that the visual system adaptively switches pooling strategies depending on whether there is a local 2D solution.

Figure 5. A velocity-space representation of local motion signals being combined using IOC and VA methods. This representation is different to Figure 1, which was concerned with extracting a single (local) motion component (direction) from an object. Instead, this representation shows how these extracted velocities are combined into a single, global solution by equating the starting location for all vectors. The left panel shows Type 1 motion where component motion directions (C1 and C2) lie on the opposite side of the y-axis where both IOC and VA make the same global motion prediction. The right panel shows Type 2 motion where both components are on the same side as the y-axis producing different IOC and VA solutions.

1.1.3 Neurophysiology of motion processing

There is very strong evidence from both humans and primates showing that global motion is integrated in area MT of macaques (Britten et al., 1993; Majaj et al., 2007; Movshon and Newsome, 1996; Newsome and Paré, 1988; Rust et al., 2006) and its functional equivalent, V5, in humans (Cowey et al., 2006; ffytche et al., 1996, 2000; Morrone et al., 2000; Rees et al., 2000). This area receives most of its input from V1, with almost all neurons show direction-selective responses rather than responses to shape and texture (Born and Bradley, 2005). There is also significant evidence for direct
connections between LGN and V5, which cause a fast response (within ~60 ms of stimulus presentation) that bypasses V1 (ffytche et al., 1996; Laycock et al., 2007; Stevens et al., 2009).

V5 has large receptive fields each covering a large amount of the visual scene (~10°) making them well suited for pooling multiple motion signals into a single neural response (Born and Bradley, 2005). Neurons in this area produce very different and complex responses compared to earlier stages of the processing hierarchy. For example, when viewing a plaid stimulus, some neurons (between 23% and 86%) in this area respond to individual (component) motion directions, while other neurons (between 8% and 68%) respond to the combined (IOC or VA) motion direction of the plaid that corresponds to the perceived direction (Albright, 1984; Gharaei et al., 2013; Kumano and Uka, 2013).

Areas V3a and MST have also been shown to be involved in global motion integration (Braddick et al., 2001; Duffy and Wurtz, 1991a,b; Harvey et al., 2010; Tootell et al., 1997). Like V5, V3a responds very strongly to global motion (Braddick et al., 2001) and also seems to detect more complex aspects of motion, including determining the position of moving objects (Harvey et al., 2010), responding to objects moving in depth and possibly incorporating form information (Backus, et al., 2001), from curvature information in motion computation (Caplovitz and Tse, 2006). MST, which is higher in the processing stream than V5, has been shown to be highly responsive to large-scale optic flow fields that extend over very large areas (Duffy and Wurtz, 1991a,b).

Overall, because of the evidence outlined so far, motion processing appears to be at least a two-stage process. The first stage is local motion detection where changes in luminance and contrast generate motion signals. These local motion signals will be
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ambiguous if originating from rigidly-translating extended contours and need to be combined (using IOC, VA or FT) with other local estimates to derive veridical global motion direction in the second stage of global integration (Heeger, 1987; Heeger et al., 1992; Morrone et al., 1995. There is also evidence that motion signals can input directly from LGN into V5, before feeding back into V1. However, the role of this connection in perception currently remains unclear (Laycock et al., 2007; Stevens et al., 2009).

1.2 Form-motion interactions

As previously discussed, the standard conceptualization of motion perception generally occurs without reference to form information, and, therefore, does not predict interactions between the two supposedly separate processes. In contrast to this viewpoint, in this section, I will outline evidence that form information affects three central tasks for the motion system: detecting motion, deriving motion direction from this signal and, finally, integrating multiple direction estimates into a single representation

1.2.1 Form changes that generate motion

A number of studies have found that when a small square instantaneously changes to a long bar motion is perceived in the direction required to explain the shape change (Hikosaka et al., 1993a,b). This is known as illusory line motion (ILM; see Figure 6 for a schematic example, also see Movie 1 in Chapter 2). Observers report the shapes do not appear to instantaneously change from one to the other but rather appears to smoothly grow in the direction of shape change.
Figure 6. A schematic representation of ILM showing a small square being replaced by a long bar. The bar appears to grow from left to right in this stimulus configuration.

A high-level attentional gradient hypothesis was originally proposed to explain this effect, suggesting that attention is summoned to the small square when it is presented. This speeds processing in the immediately attended area, falling off rapidly with distance (Hikosaka et al., 1993a,b). Because of this enhancement, when the long rectangle is presented, motion detectors respond to the region of the small square before more distal regions. This results in the perception of smooth motion away from the square. This attentional gradient can be caused by visual, auditory and somatosensory cueing (Shimojo et al., 1997). However, a number of studies that were published in the following years challenged this explanation (Christie and Klein, 2005; Downing and Treisman, 1997; Hock and Nichols, 2010). These studies showed that a simpler filling-in process, which is underpinned by standard motion energy-based principles, could account for the motion percept. Downing and Treisman (1997) showed ILM is not
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dependent on attentional factors and is, instead, likely to be accounted for by the conventional motion energy-based system. Additionally, an experiment using a modified version of ILM, which controlled for spatial factors showed, motion is still perceived in the same direction regardless of where attention is allocated (Hock and Nichols, 2010). These results strongly suggest that ILM can often be accounted for by the existing low-level motion energy mechanisms, not the purported high-level attentional system.

Tse et al. (1998) developed a more complex version of ILM, called transformational apparent motion (TAM) that appears to provide stronger evidence for form-based motion perception. The typical TAM stimulus (Figure 7, also see Movie 2 and 4 in Chapter 2) has two separate, but overlapping, shapes that are discretely presented. Observers report the first shape appears to smoothly morph into the second shape rather than an abrupt transition between shapes.
Figure 7. An example of the two frames of a stereotypic TAM stimulus, with the arrow indicating the perceived motion direction when frame instantaneously changes into frame 2. The red dots indicate the central luminance distribution of the object in both frames. Motion is perceived to go from left to right when the shape changes from the first to second frame. The motion energy signature, however, moves in the opposite direction, as indicated by the change in the centroid position between the frames. Modified from Tse et al. (1998).

Unlike ILM, under certain stimuli configurations, TAM cannot be explained by low-level motion energy mechanisms. For TAM to be perceived, form information must first be analyzed in both the initial and end shapes. Tse argues this form analysis process simultaneously occurs in the ventral pathway with the computation of motion signals in the dorsal pathway, with the form signal constraining the motion solution. Consistent with this hypothesis, TAM appears to activate normal motion processing areas (V5), in addition to form processing areas (LOC; Tse, 2006). However, the stimuli used in the study (a more complicated ILM stimulus) did not control for motion energy with the perceived direction being consistent with the energy direction. The finding,
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therefore, does not fully establish that TAM activates motion sensitive areas after controlling for motion energy.

Caplovitz and Tse (2006) argue that TAM can only be perceived after a form-motion interaction has taken place and, thus, that there is a separate high-level processing stream driven by contour analysis and feature tracking in addition to the low-level motion energy stream. The high-level nature of TAM was emphasized by the motion percept arising after 3D shape (a high-level process) information has been extracted (Tse and Logothetis, 2002). Tse and Logothetis (2002) found the defining feature that separates TAM and translational AM is the smooth change and continuous change from the initial to the end shape. This difference arises because typically figures do not overlap in translational AM whereas in TAM they do. Because of this, the visual system must first parse figures from the background them match them across space and time.

Overall, the TAM results uniquely show that form information can cause motion to be signaled in a manner independent of the standard motion-energy accounts of motion extraction. Some evidence has been provided that form information may input the motion system by the stage of global motion pooling. Although, the locus and mechanism of this interaction has not yet been conclusively established when carefully controlling for low-level stimulus properties.

1.2.2 Orientation influences motion direction

The previous section presented evidence that form information may provide a unique input into the motion system that is unpredicted by the dominant motion energy models (Adelson and Bergen, 1985). The next section will examine how form information also affects the next stage of processing where direction information is extracted from this signal. This section will do this presenting evidence showing that
orientation information (possibly entering the motion system in the same manner outlined in the previous section) can influence this direction processing.

Geisler (1999) argues form information arising from the response properties of V1 neurons can allow directionally ambiguous local motion signals, subject to the aperture problem, to be converted to unambiguous 2D motion signals. The theory argues that the ~100 ms integrated time of visually-selective V1 neurons causes fast moving objects to leave an oriented form cue along the axis of the travel, known as a ‘motion streak’, that is rarely perceived (Burr, 1980). Geisler (1999) argued that narrowly-tuned orientation-selective neurons in V1 detect the static form cue from the motion streak and multiplicatively combine this information with the motion signals which are subject to the aperture problem (Figure 8). This multiplicative combination allows the motion signals to inherit the precision of the orientation information, effectively converting the 1D signal into a 2D signal.

![Motion-selective neuron](image1)

![Orientation-selective neuron](image2)

**Figure 8.** A schematic diagram showing Geisler’s (1999) proposed mechanism for motion streaks. The motion-selective neuron in the top panel will detect and respond to any motion within a 180° arc, thereby being subject to the aperture problem. The perpendicular orientation-selective neuron detects the motion streak. The outputs of these two neurons are multiplicatively combined giving the motion signal the directional precision of the orientation signal.

Figure 9 shows an example of the theorized cortical representation of streaky
motion. There has now been considerable neurophysiological and psychophysical
evidence for the hypothesis that fast motion will leave a form cue in early visual areas.
In his original demonstration, Geisler showed that motion streaks, aligned with the axis
of motion, increase contrast sensitivity for motion that was parallel, but not
perpendicular, to oriented noise, suggesting that the form cues from the streak were
being masked. Basole et al. (2003) and Geisler et al. (2001) showed that fast motion
causes responses in V1 neurons oriented parallel to the motion direction, whereas slow
motion only causes activation in perpendicularly-oriented neurons. A human functional
imaging study supported these resulting finding that fast, streak-causing motion
produces greater activation in V1 than slow motion which would likely produce fewer
streaks (Apthorp et al., 2013). In addition, adapting to fast-moving stimuli repels the
perceived orientation of a subsequently-presented static grating, similarly to the tilt
aftereffect (Apthorp and Alais, 2009). This effect suggests that the motion streak itself
was adapting orientation-selective mechanisms causing the orientation repulsion.
Evidence has also been presented suggesting that the motion streak is treated
comparably to standard static orientation, showing similar spatial frequency and
orientation tuning properties (Apthorp et al., 2009, 2010, 2011). Furthermore, the
stimuli creating the neural smear can be either a luminance-defined first-order cue or a
contrast/texture-defined second-order cue (Badcock and Dickinson, 2009).
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Figure 9. An example of how the extended integration time (in this case exposure duration) causes a moving object to leave an oriented form cue along the axis of motion. Photo by Lotus Carrol (https://www.flickr.com/photos/thelotuscarroll/14106451215). Used under a Creative Commons license.

Following Geisler’s initial demonstration, Ross et al. (2000) showed that presenting successive locally-uncorrelated patterns with a consistent global pattern orientation, results in perception of motion in the global orientation direction. The stimuli, known as dynamic Glass patterns are created by presenting successive Glass patterns, made up by randomly positioning dot pairs aligned along a common global orientation (Figure 10 (and corresponding Movies 1a-1d), Glass, 1969; Glass and Perez, 1973). Rapidly presenting many versions of Figure 10a (Movie 1a) will result in the perception of translational motion even though the dot pairs making up the glass pattern are randomized in each version. Presenting successive, locally uncorrelated patterns is thought to produce undirected motion energy, which is channeled by the global pattern information to produce motion in the pattern direction (Ross et al., 2000). However, unlike Geisler (1999) who argued that these form-motion interactions take place in V1,
Ross et al. (2000) argued that the motion percept results from orientation information, detected in V1, being combined with the undirected motion information in V5. Consistent with Ross et al.’s proposal, presenting static noise parallel to the pattern orientation decreases sensitivity to the motion signal (Burr and Ross, 2002).

Figure 10. Four examples of (a) translational, (b) concentric, (c) spiral, and (d) radial glass patterns. See corresponding movies for the dynamic glass effects where motion is perceived in the pattern direction.

Earlier work showing that fast motion causes orientation cues does not itself conclusively support Geisler’s hypothesis that form and motion is multiplicatively combined in early visual areas, as the interaction with these signals could be fed forward to a higher visual stage. Indeed, in both macaques and humans, dynamic Glass patterns have been shown to activate motion sensitive areas (Superior Temporal Sulcus...
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and V5/hMT, respectively) (Krekelberg et al., 2003, 2005). This coincides with previous studies showing that static images that imply movement activate V5/hMT in humans (Kourtzi and Kanwisher, 2000; Senior et al., 2000) and biological motion with coherent form causes greater activation in Superior Temporal Sulcus than with incoherent form (Beauchamp et al., 2003; Grossman et al., 2000).

Dynamic Glass patterns appear to show that form processing provides an early bottleneck with thresholds showing similar biases for different pattern types (i.e. spiral, translational, concentric) for both static and dynamic Glass patterns, which is different to standard global dot motion (Dickinson and Badcock, 2009; Nankoo et al., 2012). This pattern of results may be because for dynamic Glass patterns the form signal is necessary to perceive motion directed in the pattern direction. Coherence thresholds for Glass patterns (Wilson and Wilkinson, 1998; Wilson et al., 1997) are higher than those for global dot motion (~25% compared to <10%; Baker et al., 1991; Edwards and Badcock, 1995; Newsome and Paré, 1988), meaning that as coherence decreases, the form system will cease providing global pattern information before the motion system ceases providing a global motion signal. This means that coherence thresholds for determining dynamic Glass pattern direction are constrained by form, not motion, sensitivity leading to thresholds being comparable with form, but not motion stimuli. Therefore, the current evidence does not definitively test one of the central predictions from the motion streak hypothesis of how orientation and motion information are combined to signal direction. The evidence presented could be consistent with form and motion being multiplicatively combined in V1, or instead that the interaction with the orientation cue, gathered at V1, occurring downstream at a later processing stage.

Regardless of the exact manner that orientation and motion signals interact, both models predict that orientation cues affect perceived motion direction. Indeed,
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presenting extended lines that are not oriented along the axis of motion attracts the motion direction towards the orientation of the lines (Krekelberg et al., 2003; Lorenceau et al., 1993; Ross, 2004). Similarly, the perceived direction of fast motion can be either attracted or repelled away from the orientation of background lines (Anstis, 2012; Khuu, 2012; Khuu and Kim, 2013). A motion streak-like mechanism can also explain the perceived direction in the classic barber pole illusion. In the illusion, motion is perceived to move vertically along an elongated rectangle regardless of the carrier orientation (Wallach, 1935). However, if the local orientation of the aperture is changed, or surrounding oriented lines are added, the motion is perceived along the orientation axis (Badcock et al., 2003; Kooi, 1993). The direction of the Barber Pole illusion can be explained by the edges acting as motion streaks because these will convert the ambiguous motion estimate to signal direction along the orientation axis.

An object’s orientation also influences its perceived speed. The perceived speed of a translating object is increased when its orientation is consistent with the motion direction but, conversely, decreased when the orientation is perpendicular (Blair et al., 2014; Caplovitz et al., 2006; Georges et al., 2002; Porter et al., 2011; Series et al., 2002). This change in speed with object shape is likely why the path of an object appears distorted along the object’s orientation (Magnussen et al., 2013, 2014). It is also likely that the same motion streak mechanism can describe these results with the orientation information of the shape increasing the response to the motion directions on the orientation axis. This will increase perceived speed if velocity is directly related to the magnitude of activity in the relevant direction-selective channels.

Taken together, the surveyed literature shows the large impact orientation can have on the perceived speed and direction. These effects would not be predicted by the standard models of visual processing which argue for separate form and motion
processing but could be predicted by either motion streak model (either that provided by Geisler (1999) or Ross et al. (2000)).

1.2.3 Form can assist motion pooling

After the visual system has extracted the motion direction for each local signal, this information must be combined with other signals originating from the same object to indicate global motion. This is one of the key challenges of the visual system, as the correct motion signals must be assigned to the same object that caused them, while avoiding integrating signals from different objects. Form information could be potentially useful in this task, as motion alone does not necessarily give the veridical direction of an object. For example, low-contrast signals are perceived to move slower than high contrast signals (Dougherty et al., 1999; Hürlimann, Kiper, & Carandini, 2002; Thompson, 1982; Thompson et al., 2006). Thus, if one enters an environment with speckled light (i.e. a forest) this may cause the same object to have both high- and low-contrast parts. This could potentially cause motion signals to be incorrectly assigned to separate objects if the process is based on motion information alone (see Figure 11). For this reason, it could be useful for the visual system to use the object’s shape to help correctly pool and segment the relevant motion signals.
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Figure 11. Two examples of how motion components belonging to a single object are decomposed in velocity space depending on luminance levels.  

**a.** Rigid motion cause all vectors associated with an object to fall on a circle in velocity space. The true 2D direction corresponds to the diameter and rotation of the circle relative to the axis origin. No vector will fall off the circle in situations with consistent luminance.  

**b.** The same rigid motion in velocity space but in inconsistent luminance levels. The blue vectors are parts of the objects in high luminance, leading to increased perceived speed, while the red vectors are in low luminance levels leading to the converse affects. This causes some components too fall off the circle.

This section will review evidence showing how form information affects motion recovery at both local and global levels. A recent series of studies suggested that early stages of motion processing might use form information to overcome limitations in local motion signals imposed by the aperture problem. Multiple local motion signals are combined using various computational strategies (e.g. IOC, VA) to overcome directional uncertainty imposed by the small receptive field sizes of V1 neurons. The visual system appears to adaptively switch between these pooling solutions depending on the type of local motion signals (Amano, et al., 2009). If the signals are 1D (and are thus subject to the aperture problem) then the IOC solution is used; whereas 2D signals (which are not subject to the aperture problem) are pooled using VA. Form information appears to resolve the directional uncertainty imposed by the aperture problem. When
orientation cues are added to 1D stimuli then the pooling solution switches from IOC to VA (Edwards, et al., 2012), suggesting the signals have been converted to 2D and are, thus, no longer subject to the aperture problem. It is possible that the orientation information could be interacting with the local motion signal through Geisler’s (1999) proposed motion streak mechanism.

Form information also appears to influence processing at the stage of global motion recovery. Figure 12 (also see Movie 1 in Chapter 6) shows a schematic diagram of the main stimuli used to show how this interaction occurs. The stimulus is a diamond rotating behind four apertures, where the observer can only see a number of spatially-separated lines translating behind apertures. Lorenceau and colleagues have shown that, in some circumstances, observers perceive an occluded diamond as moving globally while other times they will perceive the local motion of the line and have no awareness of a diamond moving (Caclin et al., 2012; Lorenceau, 1998; Lorenceau and Alais, 2001; Lorenceau and Lalanne, 2008; Lorenceau and Shiffrar, 1992, 1999; Lorenceau et al., 1995). The different percepts are associated with a complex interplay in the visual system. Stimulus configurations leading to integration yield a larger BOLD response in the ventral areas strongly associated with form perception (LOC) and decreased response in motion-sensitive dorsal areas (V1, V5) compared to configurations leading to segmented line motion (Caclin et al., 2012; Fang, Kersten, & Murray, 2008; Murray, Kersten, Olshausen, Schrater, & Woods, 2002). This finding is consistent with the subjective impression of a translating solid shape during integration that is absent during segmentation.
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Figure 12. a. Two examples of how form can assist in global motion recovery. The pairs of lines opposite each other move with sinusoidal drift rates in the same phase whereas the phase of the drift rates of the other pair of lines is offset by 0.5 cycles (shown in b). This gives the impression of either diamond rotating (the global interpretation) or two sets of translational lines (the local interpretation). Lorenceau and Alais (2001) found that the shape of object moving behind the aperture determined whether the observers saw the global or local interpretation of the motion. Adapted from Burr and Thompson (2011), see (http://www.perceptionweb.com/perception/perc0801/square.html) for interactive examples of this stimulus.

A number of low-level factors have been found that bias the percept towards either segmentation or global motion. For example, presenting the lines at low contrast (Lorenceau & Alais, 2001; Shiffrar & Lorenceau, 1996), in the periphery (Lorenceau & Alais, 2001) or for a short durations (Shiffrar & Lorenceau, 1996) tend to cause the stimulus to appear to be globally translating along a circular path. Because of these findings it was originally argued that classification and salience of terminators (which would be affected by the aforementioned factors) determined whether the stimulus was seen as integrated or segmented (Lidén and Pack, 1999; Shiffrar and Lorenceau, 1996).
Line terminators can be classified as belonging to either a target object (intrinsic) or an overlapping object (extrinsic; Shimojo, Silverman, & Nakayama, 1989). When terminators are classified as intrinsic, they convert the motion from 1D to 2D (Lorenceau and Shiffrar, 1992). A 2D motion vector of each line segment in the occluded diamond stimulus would give the translational motion perpendicular to the contour. This is consistent with the segmented percept of the occluded diamond stimulus. If the terminators are not salient then the motion vector for each line remains 1D meaning the motion system needs to pool across the four vectors from the contours resulting in the global motion percept (Lorenceau and Alais, 2001; Lorenceau and Shiffrar, 1992).

However, this does not seem to be a wholly adequate explanation as the global context of the occluding objects is taken into account when determining which elements are pooled or segmented rather than just the edges (McDermott and Adelson, 2004; McDermott et al., 2001). These authors demonstrated this by showing that shape information, distant from the junctions between shape and aperture edge, markedly affect whether the shape is seen as integrated or segmented. This result suggests that the changes for this stimulus cannot be entirely due to the classification of terminators and is, instead, subject to some global form constraints.

Lorenceau and Alais (2001) provided evidence that an object’s shape determines whether the local elements would cause the motion signal to be globally integrated. They showed that lines implying a shape with a closed contour (e.g. a diamond) would be globally integrated while shapes with open contours (e.g. a cross) would not. Later studies, however, suggested that this distinction between open and closed contours also does not appear to be a comprehensive account of the switch between integrated and segmented percepts (Kane et al., 2009, 2011) as coherent motion can come from
stimuli, viewed behind an aperture, that does not form closed contours.

One possible explanation for the difference between these studies could be the engagement of selective attention. The diamond stimuli used by Lorenceau and colleagues is presented behind four apertures, whereas Kane and colleagues presented stimuli behind many (>80) apertures. As selective attention can only simultaneously track four items (Intriligator, 2001; Pylyshyn and Storm, 1988; Yantis, 1992), observers could attend to each side of the occluded diamond with four apertures but not when there are multiple apertures. It is, therefore, possible that selective attention may be having a detrimental effect on the integration of shapes with open contours only allowing closed contours to be bound.

Providing a particular kind of global form cue associated with the shape’s outer boundary appears to assist in overcoming the separation of motion processing mechanisms. In many instances, first- and second-order motion signals are not combined until after the stage of global motion integration (Badcock and Khuu, 2001; Cassanello, Edwards, Badcock & Nishida, 2011; Edwards and Badcock, 1995), although these signals may interact at low-contrast levels for the first-order signals (Aaen-Stockdale, Ledgeway, McGraw, & Hess, 2012). However, if the occluded diamond stimulus is made from a combination of first- and second-order cues then observers appear to be able to integrate across these inputs (Maruya and Nishida, 2010). This result is consistent with the finding that motion streaks also assist in the recovery of global motion (Edwards and Crane, 2007), suggesting that form cues can enhance global motion sensitivity and overcome processing limitations. Adding a form cue could effectively convert an ambiguous 1D motion signal to an unambiguous 2D vector (Edwards et al., 2012).
1.2.4 Summary of form-motion interactions

The previous section examined the growing evidence showing that form and motion can interact at relatively early processing stages. These interactions can cause the perception of motion, unrelated to the low-level motion energy, change perceived motion direction and assist in motion pooling. The TAM literature, taken together with the results just discussed, suggest that the visual system may be able to use form information to derive motion information and solve pooling and segmentation problems. These studies also suggest that there could be reciprocal interactions between global form and motion processing areas in the ventral and dorsal pathways that have yet to be fully elucidated.

1.3 Thesis Outline

The overall aim of the thesis is to investigate how form information assists in the recovery of motion signals. This interaction will be examined on three main tasks of the early to mid-level motion system: extracting motion in the environment, deriving motion direction from this information, and integrating local motion signals over space. Specifically, in the first study it will be shown that form information, which causes the perception of motion, enters the motion system by the stage of global motion extraction. Following this, it will be shown that orientation information caused by the extended integration time of visually-selective neurons in V1 (known as motion streaks) influence motion direction at the stage of global motion pooling (most likely in V5), not V1 as previously thought. A model is proposed to explain this pattern of results which is examined in more detail in the next two studies. First, it is demonstrated that orientation information leads to direct, and previously unaccounted for, gain modulation of neurons at the stage of global motion extraction. Second, it will be shown that the shape of a moving object will change its perceived motion direction, in a manner predicted by the
model. Finally, it will be shown that form information that enters the motion system in the manner described by the model influences how motion signals are integrated – one of the fundamental tasks of the visual system.

I will now outlined in more detail the experimental chapters contained in this thesis. The first study (Chapter 2) examines whether multiple objects undergoing form changes leading to the perception of TAM can be globally integrated into a single perception of motion. This is a pertinent question because currently TAM has only been casually described with demonstrations showing the conditions under which it occurs (Tse et al., 1998; Tse, 2006; Tse and Logothetis, 2002). The reason why it occurs and where this unique motion signal enters into the visual system has yet to be fully elucidated. This is likely because the low-level properties of the stimulus are difficult to manipulate while still perceiving illusory motion. We dealt with this issue by placing multiple TAM elements into an array and investigating whether they yield a coherent, global motion percept. This allowed us to show that these stimuli, like conventional motion, can be integrated into a single global motion precept. This global integration demonstrates that the form information that drives the TAM percept likely enters the motion system by, at least, V5, which is essential for global motion perception.

The next study (Chapter 3) built upon the finding that form information appears to have a direct input to the motion system, separate from the motion energy-based system; suggesting that form information alone can cause motion to be detected. To re-iterate, following the initial detection of motion, motion direction must be extracted. An influential model (Geisler, 1999) suggested that form information, from the extended integration time of neurons in V1, may be useful for this task. We tested this model using a visual aftereffect, where after adapting to a static oriented grating, the perceived direction of subsequently-presented, streak-causing motion is repelled away from the
adapted orientation. We showed the angular dependence of this aftereffect, which would be caused by changes to the motion streak mechanism, is double that compared to when static form stimuli are used for the test. This is contrary to Geisler’s (1999) model as the motion streak should have the same proprieties as form, and instead suggests the form information is entering the motion system at a later stage, most likely V5 or MST. Later experiments supported this observation as the aftereffect was found to change from repulsive to attractive when the spatial frequency of the adaptor was varied, unlike for form. This again suggests the orientation information was entering the motion system at the stage of global integration as this area integrates across a broad range of spatial frequencies, unlike V1, which remains spatial-frequency selective. Using transcranial direct current stimulation, we confirmed to role of V1 in the aftereffect in addition to V5. Because of these results, we proposed a new model of motion streaks where orientation-selective neurons in V1 exert either inhibitory or excitatory gain onto neurons at the stage of global motion pooling, which influences the perceived direction of motion. This model provides a new mechanism for orientation information to influence motion perception.

Chapter 4 provided a strong test of the aforementioned model. The model predicts that any orientation information, not just from motion streaks, will modulate the gain of the motion-selective neurons at the stage of global motion pooling. To test this prediction, we showed that adapting to static orientation changed the perceived direction of motion in a manner that cannot be due to changes in the representation of local motion. The motion stimulus was the global plaid array (Amano et al., 2009a,b; Edwards et al., 2012; Johnston and Scarfe, 2013), which consists of multiple plaid elements whose orientation is randomly-allocated but the drift rates of each individual plaid is made to be consistent with a globally-defined IOC direction. This stimulus
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gives the strong impression of motion in the global direction. The change in perceived
direction of this resultant motion following adaptation to static gratings cannot be due to
local aftereffects because the orientations of the plaids are randomized over 180° which
means that the local aftereffects will average out to 0°. We found the angular
dependence of this aftereffect was similarly broad as the motion streak aftereffect
(Chapter 3), which again suggests that orientation is affecting the stage of global motion
integration. We next replicated the spatial-frequency dependency of the motion streak
aftereffect, with the aftereffect changing from repulsive to attractive when the spatial
frequency of the adaptor was changed by two octaves. We then showed that gain from
adaptation directly affects the global motion integration mechanism by changing global
motion sensitivity.

Chapters 3 and 4 both used adaptation to orientation to change the perceived
direction of subsequently-presented motion. Chapter 5 builds upon these results
showing that the shape of a moving object will change its perceived motion direction.
This could be considered the form-motion equivalent of the tilt aftereffect, where the
perceived orientation of a line is repelled away from the adapting orientation (Gibson
and Radner, 1937; Ware and Mitchell, 1974). The tilt illusion is similar to the tilt
aftereffect, with the orientation of surrounding lines changing the perceived orientation
of a test line (Clifford, 2014; O’Toole and Wenderoth, 1977). Chapter 5 presents the
form-motion equivalent of the tilt illusion where simultaneously-presented orientation
(either intrinsic or extrinsic to the stimulus) changes the perceived direction over a
moving stimulus. Furthermore, similar to the results in Chapters 3 and 4, the perceived
motion direction can be attracted or repelled depending on the spatial frequency of the
orientation cue. Using this contextualization of a form-motion interaction, we showed
the model could predict four previously-published psychophysical illusions (Anstis,
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2012; Badcock et al., 2003; Farrell-Whelan and Brooks, 2013; Ross, 2004) showing that form information changes perceived motion direction. These results suggest that form information influences motion direction processing in the manner specified by our form-motion model.

Chapter 6 builds upon the previous results showing how the shape of an object influences how motion signals are integrated or segmented into separate sources. A modified version of Lorenceau’s (Caclin et al., 2012; Lorenceau and Alais, 2001; Lorenceau and Shiffrar, 1992) occluded-aperture stimulus was used to do this. This stimulus was modified so the boundary was made from Gabors in static envelopes to define the edges of the shape, with the drift rates of the carriers made to be consistent with a globally-defined IOC motion solution. This stimulus allowed us to keep the low-level motion information consistent throughout conditions while altering the form information. It was found that the fidelity of low-level motion information determined whether these stimuli were integrated or segmented. This was done by showing that shapes with three or four sides were segmented while those with more sides were integrated. Increased integration is shown to arise because the number of represented motion directions exceeds motion transparency limits (Edwards and Greenwood, 2005; Greenwood and Edwards, 2006, 2007). When there are three or four sides there are two or three motion directions represented. Each direction results in a population response that is distinguishable from the other directions, leading to motion segmentation. The population response becomes indistinguishable when there are more directions represented leading to motion integration. Following this, it was found that the form information does not add any increase in sensitivity to global motion signals if the shape forms a closed contour. Instead, form information will only prohibit motion integration if the shape forms an open contour.
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Overall, the experiments presented in this thesis first show that form information enters the motion system at the stage of global motion integration. These findings are then described by a model of the mechanism of form-motion interaction, where orientation controls the gain of motion processing along an axis. This model is assessed and confirmed in the next two studies showing that orientation directly modulates the gain of motion-selective neurons at the stage of global motion integration and that the shape of an object changes its perceived motion direction. The final study examined how form information, entering the motion system in the specified manner, influences motion integration.
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2 The shape of motion perception: Global pooling of Transformational Apparent Motion

Matthew F. Tang¹, J. Edwin Dickinson¹, Troy A.W. Visser¹,
Mark Edwards² & David R. Badcock¹

1. School of Psychology, The University of Western Australia, Crawley, WA, Australia
2. Research School of Psychology, The Australian National University, Canberra, ACT, Australia

2.1 Abstract

Transformational apparent motion (TAM) is a visual phenomenon highlighting the utility of form information in motion processing. In TAM, smooth apparent motion is perceived when shapes in certain spatiotemporal arrangements change. It has been argued that TAM relies on a separate high-level form-motion system. Few studies have, however, systematically examined how TAM relates to conventional low-level motion energy systems. To this end, we report a series of experiments showing that, like conventional motion stimuli, multiple TAM signals can combine into a global motion percept. We show that contrary to previous claims, TAM does not require selective attention and instead multiple TAM signals can be simultaneously combined with coherence thresholds reflecting integration across the entire stimulus area. This system is relatively weak, less tolerant to noise, and is easily overridden when motion energy cues are sufficiently strong. We conclude that TAM arises from high-level form-motion information that enters the motion system by, at least, the stage of global motion pooling.
2.2 Introduction

Considerable psychophysical and neurophysiological evidence indicates that different neural pathways and cortical regions process form and motion (Goodale & Milner, 1992; Livingstone & Hubel, 1987; Ungerleider & Mishkin, 1982). There is, however, a growing body of research showing that form and motion can interact. In biological motion, for example, the relative motion of a small number of dots gives the vivid impression of a moving figure (Johansson, 1973, 1976). Evidence suggests that the same global form mechanism is sensitive to shape information and shape information derived from illusory displacement in perceived position (Dickinson, Han, Bell, & Badcock, 2010). Motion streaks, arising from the extended temporal integration period of neurons in early visual cortex, improve global motion discrimination (Edwards & Crane, 2007) and provides a form cue in the direction parallel to the motion signal which can refine direction estimates (Apthorp et al., 2013; Badcock & Dickinson, 2009; Barlow & Olshausen, 2004; Burr & Ross, 2002; Francis & Kim, 2001; Geisler, 1999; Ross, 2004; Ross, Badcock, & Hayes, 2000). Providing form cues indicating a closed contour also enhances recovery of the global motion direction compared to an open contour (Lorenceau & Alais, 2001; Lorenceau & Lalanne, 2008). In addition, form information provided by the aperture edge of an ambiguous motion signal dramatically changes the direction of perceived motion (Badcock, McKendrick, & Ma-Wyatt, 2003; Beutter, Mulligan, & Stone, 1996; Kooi, 1993), and orientation of the first-order carrier texture alters the perceived direction of motion of a second-order envelope (Cropper & Badcock, 2008). Moreover, an object’s shape and orientation influences its perceived speed, as objects appear to be moving faster when aligned to the motion direction (McCarthy, Cordeiro, & Caplovitz, 2012; Seriès, Georges, Lorenceau, & Frégnac, 2002). Finally, and most surprisingly, adapting to still images that depict movement
purportedly generates the motion aftereffect when tested with real motion stimuli (Winawer, Huk, & Boroditsky, 2008).

Apparent motion arises when two spatiotemporally separated objects are presented in succession, leading to the percept of a single moving object (Exner, 1888). Ambiguity in apparent motion displays can arise when more than two objects are present, forcing the visual system to decide which objects are matched (Anstis, 1980; Ullman, 1979). Most studies showed that shape and color have little effect on this matching, supporting the traditional separation between form and motion processes (Kolers & Pomerantz, 1971; Kolers & von Grünau, 1976; Navon, 1976). The dominance of spatiotemporal factors in matching is commonly referred to as the ‘nearest neighbor’ principle, which is usually consistent with a motion-energy account of motion perception (Adelson & Bergen, 1985; Chubb & Sperling, 1988). There have, however, been some demonstrations showing that form can influence matching but only after controlling for the more salient factor of spatiotemporal proximity (Green, 1986a, 1986b, 1989; Hein & Cavanagh, 2012; Hein & Moore, 2012). Form can also affect the perceived path of apparent motion after controlling for matching (Khuu, Kidd, & Badcock, 2011; Kim, Feldman, & Singh, 2011; Shepard & Zare, 1983). For example, Khuu et al. (2011) showed that orthogonally rotating the element’s orientation in a manner consistent with rigid rotation around a distant point caused the path of apparent motion to also appear curved.

Transformational apparent motion (TAM) is argued to be a unique type of apparent motion stimulus that arises when an instantaneous shape change causes the perception of motion in the direction explaining the shape change. Importantly, TAM seems to suggest that form information alone can drive the motion system. In initial
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demonstrations of TAM, originally called ‘illusory line motion’ (ILM; Hikosaka, Miyauchi, & Shimojo, 1993a, 1993b; Kanizsa, 1951), a small square instantaneously changes into an overlapping long bar leading the square to appear to smoothly morph in the direction of the elongation (Movie 1). The effect was initially thought to arise through a high-level attentional gradient with the small square acting as an attentional cue, resulting in faster processing of the surrounding space, and the consequent appearance of a growing line. Critically, however, these initial demonstrations of TAM do not require high-level processes in order to be explained and can be entirely accounted for by low-level motion energy as the perceived direction of motion is consistent with the shift of the luminance centroid (Downing & Treisman, 1997; Fuller & Yu, 2009; Kawahara, Yokosawa, Nishida, & Sato, 1996).

Movie 1. Shows an example of ILM, the original description of TAM. This example consists of discrete overlapping form cues, with a small square alternating with a bar. The perceived direction of motion explains the shape change.

Following this initial description of form-induced motion, Tse and colleagues (Tse & Caplovitz, 2006; Tse, Cavanagh, & Nakayama, 1998; Tse & Logothetis, 2002) developed the now stereotypic TAM stimulus where motion is perceived in the direction opposite to motion energy (Movie 2). They also showed that certain versions of TAM can violate the nearest-neighbor principle with matching instead following Gestalt-like grouping rules rather than spatiotemporal proximity (Tse et al., 1998). In these displays, multiple shapes are simultaneously perceived to morph in directions that maintain contour continuation rather than following spatiotemporal proximity. The
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high-level nature of the system was further confirmed by showing the form information driving the percept of TAM occurs after the stage of 3D shape processing (Tse & Logothetis, 2002). On the basis of these results, Tse and colleagues concluded that TAM is processed in a separate high-level form-motion stream, which is not dependent on low-level motion energy (Tse & Caplovitz, 2006; Tse et al., 1998; Tse & Logothetis, 2002). Relatively little experimental work has, however, examined how this high-level system interacts with the low-level and well-described energy motion system (Lu & Sperling, 1995).

Movie 2. The stereotypical TAM stimulus that Tse and colleagues (1998) claim cannot be explained by low-level motion energy detection. The small block on the left appears to grow into the large blob on the right following shape change. The location of the luminance centroid of the shape was found in each frame (indicated by the black dot), which moves 6 pixels left (~10% of frame length) from the first to the second frame. Motion is thus perceived in the direction opposite low-level motion energy predictions.

One way to investigate this issue is by examining how multiple local TAM motion signals integrate into a global percept of motion, a phenomenon which has been well investigated with conventional motion stimuli (eg. Baker, Hess, & Zihl, 1991; Newsome & Paré, 1988). Spatiotemporally-oriented neurons in early visual cortex initially detect local motion in the environment, but the small size of their receptive fields (~ 1º of visual angle) leads to the well-known aperture problem where individual neurons cannot signal the veridical direction of 1D stimuli (Adelson & Movshon, 1982; McCool & Britten, 2008). Pooling multiple local motion signals in a higher stage,
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referred to as global motion pooling, is thought to solve this problem (Adelson & Movshon, 1982; Amano, Edwards, Badcock, & Nishida, 2009). Area V5/MT, where receptive fields are approximately ten times larger than in V1, is important for global motion integration, responding strongly to both global motion signals (Born & Yu, 2005; Kohn & Movshon, 2004; Smith, Snowden, & Milne, 1994) and apparent motion sequences (Sterzer, Haynes, & Rees, 2006; Wibral, Bledowski, Kohler, Singer, & Muckli, 2009). More recently, global motion stimuli have also been shown to strongly activate area V3a (Braddick, O'Brien, Wattam-Bell, Atkinson, & Turner, 2000; Tootell et al., 1997). The involvement of V5/MT and V3a has been confirmed as lesions and trains of magnetic pulses to these areas decreases sensitivity to global motion (Baker et al., 1991; Beckers & Zeki, 1995; ffytche, Guy, & Zeki, 1996; Harvey, Braddick, & Cowey, 2010; McKeefry, Burton, Vakrou, Barrett, & Morland, 2008; Newsome & Paré, 1988).

Given that the first- and second-order motion systems globally integrate (Badcock & Khuu, 2001; Edwards & Badcock, 1995), it would seem sensible to predict the same phenomenon would occur with TAM. The precise nature of pooling, however, may differ from that arising from first- and second-motion signals as form cues in conjunction with motion energy give the precise axis of motion (Geisler, 1999).

Previous studies have shown that although motion signals can be pooled, the pooling process depends on whether the signals are 1D or 2D (Amano et al., 2009). Form cues act to convert local motion signals to 2D, for example when motion streaks, additional lines or hard edged apertures are employed (Badcock et al., 2003; Edwards, Cassanello, Badcock, & Nishida, 2013) and suggest grouping (using form inputs which imply a 2D direction) and will be pooled using vector averaging rather than intersection of constraints. Dynamic glass patterns (a series of independently generated static glass
patterns shown in a fast temporal sequence) do not present a consistent motion energy signal but do give the impression of coherent motion consistent with the pattern type, showing the strong effect form cues can have on the perceived direction of motion (Ross et al., 2000). The perception of coherent motion in the absence of coherent motion energy suggests the form information in the Glass patterns causes the perceived axis of motion (Apthorp et al., 2013; Badcock & Dickinson, 2009; Dickinson & Badcock, 2009; Nankoo, Madan, Spetch, & Wylie, 2012).

It should also be noted that there are both theoretical and empirical reasons to believe that TAM might not act in the same manner as other motion systems. For example, Tse and colleagues (Tse & Caplovitz, 2006; Tse et al., 1998) have argued that selective attention is uniquely necessary to track the shape changes in TAM. If that is the case, global integration may be impossible as numerous studies have shown that attention limits the visual system to simultaneous tracking of a maximum of four objects (Intriligator, 2001; Pylyshyn & Storm, 1988; Yantis, 1992). Alternatively, Grossberg and colleagues (Berzhanskaya, Grossberg, & Mingolla, 2007; Francis & Grossberg, 1996) proposed that TAM results from low-level processing with form information that is extracted in V2 being passed to V5/MT where the percept of apparent motion is generated. It would be expected from Grossberg’s model that multiple TAM signals could be integrated as form information enters the motion system by the global pooling areas of V5/MT or V3a. Tse (2006) conducted a functional imaging study comparing activation between versions of illusory line motion shapes to forms with similar spatial properties but not resulting in TAM. He showed that both form and motion processing areas (V2, V3, V3a, V5/MT, LOC) show greater activation for the TAM compared to the static form stimuli. More recently, a study using
intracranial electrode recordings which, unlike Tse (2006), carefully controlled for motion energy, showed that TAM produces activation in LOC and V4 but only a weak response in V5/MT (Bertrand et al., 2012). On the other hand, if we do find that TAM globally integrates then it would suggest the form information needed for TAM feeds into the motion system by at least this level.

In a series of experiments, we examined global pooling of multiple TAM signals. We first established that multiple TAM stimuli would yield a coherent global motion percept. To do this, we developed the ‘global TAM’ array that consists of multiple TAM stimuli that are aligned with a common global direction. We initially used modified versions (referred to as “Plunger stimuli”) of the stereotypic TAM elements shown in Movie 2. When these were placed in the global array, the perceived global motion direction was in the opposite direction to TAM motion, but consistent with motion energy. A follow-up experiment confirmed these stimuli were pooled using motion energy. We then used TAM versions of Kanizsa stimuli that created a motion percept in the direction of local TAM motion, indicating they pooled using high-level TAM-related mechanisms rather than low-level motion energy. This system appears to have a much lower noise tolerance than the conventional motion energy system. A control experiment showed that the reported coherence thresholds for motion direction cannot be explained by inferences from form cues alone, suggesting that observers were indeed using the illusory motion. Finally, it has previously been argued that selective attention is needed for the high-level matching process needed in single TAM displays. We show that attention does not limit pooling in global TAM and instead observers appear to simultaneously integrate multiple signals across the entire array.
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2.3 General Methods

2.3.1 Apparatus and procedure

The stimuli were generated in MATLAB 7.2 on a Pentium PC (2.4 GHz) for all experiments. Stimuli were presented from the frame buffer of a VSG2/5 (Cambridge Research Systems) on a Sony Trinitron G420 monitor with a refresh rate of 100 Hz at a resolution of 1024 x 768 pixels (17° x 12.8° of visual angle). Observers viewed the stimuli from a distance of 102 cm making each pixel extend 1’ of visual angle with viewing distance maintained with a chinrest. Luminance was gamma-corrected using an Optical OP-200-E (head model no. 265) photometer and associated CRS software. Observing occurred in a darkened room with luminance < 1 cd/m². The background luminance of the monitor was set at 45 cd/m² and the elements were presented with a constant luminance of 90 cd/m².

All experiments employed versions of the global TAM array with the same presentation periods. Every trial began with a centrally-presented fixation dot with luminance of ~0 cd/m² displayed for 250 ms. This was followed by the two-frame global TAM array with each frame lasting 250 ms with no inter-stimulus interval. The presentation time was chosen to be well within the 100 ms integration time of single TAM elements (Tse & Logothetis, 2002). Observers made responses with a computer mouse.

2.3.2 Observers

Four experienced psychophysical observers (all males), ranging in age from 21 to 48 yrs (median = 26.5 yrs), participated in the study, with three observers included in each experiment. MT and ED are authors while all other observers were naïve to the aims of the experiments. All observers had normal or corrected-to-normal visual acuity,
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as assessed using a Snellen chart. The procedure was in accordance with the Declaration of Helsinki and approved by the Human Research Ethics Committee at the University of Western Australia with all observers providing written informed consent.

2.4 Experiment 1: TAM ‘Plungers’ stimuli pool in motion energy direction

2.4.1.1 Stimuli

Multiple spatially distributed stationary Plunger TAM elements were placed in a circular array to assess global pooling of TAM (Movie 3). The arrangement of the elements was similar to the global Gabor array (Amano et al., 2009; Cassanello, Edwards, Badcock, & Nishida, 2011), except Gabors were replaced with TAM stimuli. Forty-eight local Plunger elements, each enveloped in a 64’ x 64’ window, were arranged in an annulus with an 8.53° diameter. No TAM elements were displayed in the central 128’ of the array because the limited space in this region constrained the range of possible orientations. Analogously to global dot motion and glass patterns (i.e. Edwards & Badcock, 1995; Wilson & Wilkinson, 1998), a proportion of the elements were assigned a common global direction (clockwise or anti-clockwise rotational motion) with the remaining proportion assigned random directions. Two frames of each array were presented with all elements changing into the completed TAM shape in the second frame giving the perception of apparent motion. Under conditions of high signal and low noise, observers report the array appears to rapidly rotate following shape transformation.
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Movie 3. An example of the novel TAM global array stimuli (with a 100% coherence level) that effectively pools for a perception of global motion. In this example, the global motion direction is clockwise, which is opposite the perceived direction of motion for a single element but consistent with motion energy predictions.

2.4.1.2 Procedure

We conducted an experiment measuring the proportion of coherently-aligned local TAM elements necessary for global motion perception, using a single-interval forced-choice task to evaluate global integration. The proportion of elements coherently aligned with a common global direction instead of random directions (noise) was varied to determine the minimum signal needed to detect the direction of global motion. The method of constant stimuli (MOCS) with nine linearly-spaced levels was used to vary the signal to-noise-ratio with steps individually varied for each observer to sample the entire psychometric function. The signal elements were made to produce either clockwise or anti-clockwise rotational motion. Observers were required to indicate the direction of motion and auditory feedback was given following each response. Observation showed that auditory feedback did not alter the perceived direction. Blocks of 180 trials were completed with each observer making 100 responses for each of the nine MOCS steps. Cumulative Gaussian functions were fitted to each observer’s responses using the PAL_CumulativeNormal function in the MATLAB Palamedes
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toolbox (Prins & Kingdom, 2009), which yielded the 75% threshold. The 95% confidence interval for threshold was computed using a bootstrap procedure from Palamedes.

2.4.2 Results and Discussion

Unexpectedly, the perceived global motion of the array was in the direction opposite to the perceived individual element motion. The direction of global motion was, therefore, consistent with the low-level motion energy signals defined by centroid shifts, suggesting the global percept arises from motion energy rather than the separate high-level form-driven motion system. Figure 1 shows mean coherence thresholds for global TAM for each observer. Observers required 21% to 35% of elements moving coherently for reliable global motion discrimination. These thresholds are considerably higher than those reported for global dot motion, which are typically between 5% and 15% (Baker et al., 1991; Edwards & Badcock, 1995; Newsome & Paré, 1988), but similar to those for static glass patterns (Badcock, Clifford, & Khuu, 2005; Dickinson, Broderick, & Badcock, 2009; Wilson & Wilkinson, 1998). It is likely that some of this disparity arises because global dot motion thresholds are derived from a series (typically eight) of stimulus frames. In fact, our two-frame thresholds align well with other experiments using only two stimulus frames (Edwards & Badcock, 1995).

Figure 1. Mean coherence thresholds for all observers. Error bars indicate bootstrapped 95% confidence intervals.
2.5 Experiment 2: Plunger TAM stimuli are pooled using motion energy

The results of Experiment 1 suggest the Plunger stimuli are pooled using motion energy rather than TAM. To determine whether the motion energy signals evoked by the Plunger stimuli were being pooled, we exploited the ‘motion drag’ effect, in which the perceived position of peripherally-presented objects is spatially displaced in the direction of motion (Scarfe & Johnston, 2010; Whitney, 2006; Whitney & Cavanagh, 2000; Whitney et al., 2003). To do this, we first established that the global TAM array induced motion drag. We then measured the effects of placing a brief flash between the TAM frames, which masks conventional apparent motion by providing substantial nondirectional motion energy (Braddick, 1973). The masking occurs because the flash provides a uniform field that activates low-level motion detectors, thereby disrupting motion energy-based matching between successively presented shapes. On this reasoning, if the Plungers are being pooled using motion energy then the presentation of a flash should reduce motion drag.

2.5.1.1 Method and Procedure

This experiment used the same two-frame global array employed in Experiment 1 with the addition of two horizontally-aligned Gabors briefly presented on either side of the array coincident with the shape change (Figure 2). The procedure was based on that used by Scarfe and Johnston (2010) who showed that a global Gabor array can induce motion drag. Each peripheral Gabor was 0.83º of visual angle with a spatial frequency of 4.9 cycles per degree and a peak contrast of 84%. The phase of the Gabors was randomized for each trial. The Gabors were presented for the first 3 frames (30 ms)
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simultaneous with the TAM elements changing shape. The task required the observers to judge the relative spatial offset of the Gabors, which was controlled for using the MOCS procedure. There were nine linearly-spaced levels with the distance between each level varied between observers to allow for the entire psychometric function to be sampled. Three interleaved conditions were employed with the local TAM elements producing either clockwise, anti-clockwise or random local (unidirectional) global motion. In the clockwise and anti-clockwise condition, all elements were aligned to a common direction that results in a strong motion percept. The no-motion condition was a control condition with the direction of all elements randomized. The perceived position of the Gabors will be offset in the direction of motion if the TAM array causes motion drag. For example, in the clockwise condition, the right Gabor will generally be perceived to be higher and will, therefore, need to be physically lower to be perceived aligned with the left Gabor.

Figure 2. Stimuli from Experiment 2 measuring motion drag induced by the Plunger stimuli. (a) Shows a schematic diagram of a trial. (b) Shows an enlarged version of the second frame of the sequence which was displayed for 30 ms. In this example, the left Gabor is physically higher than the right Gabor, but will often be perceived to be lower because of the anti-clockwise motion of the global TAM array. In the flash condition of this experiment, a disk covering the area of the annulus was displayed for 10 ms immediately preceding the frame with the Gabors.
To determine whether the drag induced was due to motion energy, the same procedure was used with the addition of a white flash presented in the middle of the TAM sequence between the first and second frames of the TAM sequence. The Gabors were presented synchronous for 30 ms with the onset of the second frame of the TAM sequence where the elements changed shape, which was immediately following the bright flash. The flash, presented for one frame (10 ms) immediately preceding the shape change, had a luminance of 90 cd/m$^2$ and covered the same circular area as the global TAM array. Each observer completed 100 trials in a randomized order for each MOCS step in all conditions. Cumulative Gaussian functions were fitted to each observer’s responses for the three motion conditions in both flash and no-flash condition using GraphPad Prism (version 5.0d, GraphPad Software, San Diego, CA, USA, www.graphpad.com). This yielded the point of subjective equality (PSE) with 95% confidence intervals, indicating the degree of motion drag induced by each type of TAM array.

2.5.2 Results and Discussion

The top panel of Figure 3 shows that global TAM array produced significant drag in the direction of global motion. For all observers, the Gabors were displaced in the direction of motion energy, and opposite TAM, for both coherent motion conditions while there was no displacement for the randomized-direction condition. There was a slight response bias for observers MT and TM with the right Gabor being perceived as higher than the left Gabor in the no motion condition. This was consistent in the other two conditions with the psychometric functions shifting to the left. Motion drag differed significantly between the three conditions (one-way repeated-measures ANOVA of the PSEs, $F(2, 8) = 21.59, p < .01$). The slope of the functions also significantly increased
in the condition with the flash ($\text{Mean slope} = 0.21, SD = 0.01$) compared to the condition without the flash ($\text{Mean slope} = 0.11, SD = 0.02$), suggesting that when there is motion within the arrays it significantly reduces the ability to judge misalignment.

The bottom panel of the Figure 3 shows psychometric functions when a flash was inserted between the frames. There was significantly less drag here compared to the no-flash condition. To quantify this effect, the difference between the PSE of the clockwise and anti-clockwise conditions was found for flash and no flash conditions (Figure 4). The PSE was significantly lower when there was a flash inserted between the frames, $t(2) = 4.80, p = .04, R^2 = .92$. As the flash disrupts short-range motion energy by providing a strong omni-directional motion energy signal, this result is
consistent with the conclusion that the global Plunger stimuli are pooled using motion energy rather than high-level TAM-related motion systems.

**Figure 4.** The difference in PSE between clockwise and anti-clockwise motion in both flash (red bars) and no-flash (blue bars) conditions. For all three observers, the difference between these was significantly reduced when a flash was inserted between frames.

### 2.6 Experiment 3: TAM is pooled by a separate system

Taken together, the results of Experiments 1 and 2 indicate that Plunger stimuli are globally pooled, but using motion energy signals rather than the proposed high-level TAM system. This suggests that when multiple elements are presented, the high-level TAM system can be relatively easily over-ridden by the low-level motion energy system. However, our initial question concerning whether multiple TAM signals can be pooled into a global motion percept has yet to be answered. We used two additional TAM stimuli to answer this question. The first was derived from Baloch and Grossberg (1997), where TAM is created by morphing a bar with an illusory middle to an illusory square defined by four “Pac-man” inducers (Movie 4). As with the Plunger stimuli, the shape change of these stimuli (hereafter referred to as the ‘Kanizsa’ (1976) stimulus) displaces the centroid of the motion implied by low-level motion detectors opposite to the direction of perceived motion. But, unlike the Plunger stimuli, when the Kanizsa
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stimuli were placed in the global array they were found to pool in the direction of TAM, i.e. opposite the direction signaled by motion energy. The second novel stimulus was a variation of the illusory line motion (ILM) stimuli shown in Movie 1. This stimulus offers an interesting comparison as both motion energy predictions and TAM are in consistent direction.

Movie 4. A single element of a ‘Kanizsa’ stimulus. Like the Plunger stimulus, the centroid of the object (indicated by the black dot) moves in the opposite direction to perceived direction of TAM, but this shift is 4x smaller than in the Plunger stimulus. The centroid for each frame was found using MATLAB, which showed the centroid moved ~2 pixels left from the first to the second frame.

The purpose of this experiment was to compare global pooling between three different stimuli, pooled using TAM and/or motion energy. We first examined global motion thresholds for TAM pooling opposite to motion energy predictions (Kanizsa stimuli). This was compared to a condition where TAM globally pools in the motion energy direction but motion is perceived locally in opposite direction (Plunger stimuli). Finally, Plunger stimuli were compared to ILM where TAM and motion energy predictions are the same. If thresholds are higher for the Plunger stimuli than the ILM stimuli, it would suggest that systems underlying global TAM pooling interact with the low-level motion energy system.

2.6.1.1 Method and Procedure

Global thresholds were measured separately for each of the three stimulus types; Plungers, Kanizsa and ILM. The Plungers were the same those used in Experiments 1 and 2. The Kanizsa stimuli consisted of four non-overlapping circles, with radii of 7’.
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The stimuli were slightly rectangular with the centers of the top and bottom row of circles separated by 21’, while the centers of the left and right circles were separated by 25’. To induce TAM motion, a line with a width of four pixels and the same luminance as the background extended from the center of the lower circle to the center of the upper left circle in the first frame. For the second frame, the area between the circles was converted to an illusory square by removing a quarter of each circle, which produces the percept of the line growing into a rectangle (see Movie 4). For the ILM stimuli, a 5’ x 9’ rectangular block was changed to a 5’ x 25’ rectangular block.

To measure global TAM thresholds for the three stimulus types, we presented an array with X% of signal elements and 100-X% of noise elements (Movie 5). A SIFC adaptive staircase procedure with a three-down, one-up rule was used to estimate the 79.4% point of the psychometric function (Levitt, 1971). Observers were required to identify whether the array appeared to rotate clockwise or anticlockwise. Following previous studies of global motion (Cassanello et al., 2011; Edwards & Badcock, 1995), all staircases started with high signal levels, on this case, 100% coherence threshold (48 signal elements). Until the first mistake was made, the coherence level was reduced by eight elements following each correct response. After the first incorrect response, the step size was reduced to four, two and one for subsequent reversals and maintained at one for the final four reversals. Staircases terminated after 8 reversals with the threshold being taken as the mean coherence level of the final four reversals. Auditory feedback was given following each response before the next trial was initiated. Observers completed 10 staircases for each stimulus type in a counter-balanced order.
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Movie 5. Two versions of TAM stimuli placed in the global array with both stimuli having 100% coherence. Left panel: A TAM global array containing the Kanizsa stimuli which pool in the direction of TAM, but the opposite direction of motion energy predictions. Right panel: A global TAM array containing ILM stimuli that pool in both the direction of TAM and motion energy. The third stimulus type (Plungers) for this experiment is shown in Movie 4.

2.6.2 Results and Discussion

Figure 5 shows mean coherence thresholds for the three types of stimuli. The results clearly show that the Kanizsa stimuli integrated into a global motion percept in the direction opposite to motion energy predictions. Motion thresholds were, however, significantly higher than for either Plunger or ILM stimuli. For two observers (MT and RG), both Plunger and ILM stimuli have similar thresholds. Observer ED shows a slightly different pattern of results with thresholds for Plunger stimuli being between those for ILM and Kanizsa. The results for the Kanizsa stimuli suggest that multiple TAM signals can be integrated into a global motion percept, but noise tolerance is reduced compared to motion-energy based pooling, as indicated by the higher thresholds. Another possible explanation for this threshold increase is the greater stimulus complexity of the Kanisza figures relative to Plunger or ILM may have led to increased crowding. ILM appears to be pooled using motion energy as thresholds are similar to the Plunger stimuli and motion is in the opposite direction to the single element motion.
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Figure 5. Coherence thresholds for the three types of stimuli in Experiment 3 for the three observers. Error bars represent 95% confidence intervals.

2.7 Experiment 4: Global TAM is not due to form pooling

Although observers were asked to report the direction of the “twist” that followed shape changes, it is possible the observers were instead determining the direction of the global structure from the orientation information provided by the form cues from the TAM stimuli. To test this possibility, a control experiment was conducted to examine whether the coherence thresholds for global TAM were due to observers using the global pattern, rather than motion, information in the arrays. This was done by presenting only one frame of the TAM arrays in order to retain form information, without generating illusory motion.

2.7.1.1 Method and Procedure

The same global arrays with Kanizsa and Plunger stimuli were used as in Experiment 3 but with only one frame of the stimulus shown. Only the second frame of the Plunger stimuli was shown, while the first frame of the Kanizsa was shown for 250
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ms, because these frames gave the strongest directional cue. The second frame of the Kanizsa was rectangular and centrally placed in the inducers and therefore did not indicate whether the element was oriented clockwise or anti-clockwise. In the first frame, however, the line in the two left ‘Pac-men’ could be used to signal direction. Observers were required to indicate whether elements had a global clockwise or anti-clockwise orientation. Ten thresholds were taken for each stimulus type using adaptive staircase procedures in a counter-balanced order.

2.7.2 Results and Discussion

Figure 6 shows mean coherence thresholds for the two stimulus types. All observers could identify the global orientation direction if the signal was sufficiently high. Critically, however, thresholds for the Kanizsa stimuli were approximately 20% higher (71% vs. 49%) than in Experiment 3 when TAM motion signals were present. Thresholds for the Plunger stimuli were also higher (45% vs. 40%) than in Experiment 3, although the difference is less dramatic because the Plungers provide a much clearer orientation. This could suggest that the observers were using the orientation information from the form cues within the Plungers to determine the global motion direction rather than the illusory motion itself, although observers reported using the illusory motion for direction judgment rather than the form cues. Overall, the results clearly show that thresholds increased for static Kanizsa stimuli compared to the motion-inducing displays used in Experiment 3, suggesting that observers in Experiment 3 integrated local TAM signals to infer global motion, rather than relying on static form information only.
Experiment 5: Global TAM pooling cannot be explained by selective attention

It has previously been suggested that selective attention is needed for the spatiotemporal matching underlying perception of TAM (Tse et al., 1998; Tse & Logothetis, 2002). As spatial attention has a finite capacity as only a small number of items (possibly four) can be simultaneously tracked (Intriligator, 2001; Pylyshyn & Storm, 1988; Yantis, 1992), this would therefore imply that multiple TAM signals should not be globally integrated. On this account, the relatively high thresholds found for the global Kanizsa TAM stimuli may reflect the fact that observers derive the motion direction by selectively monitoring small regions of space rather than integrating motion signals across the display. One way to assess the possibility is to measure thresholds while increasing the number of individual elements in an array. Thresholds for both conventional global form and motion pooling show a dependence on the number of local elements in an array, increasing by increasing the total number of elements when the area is held constant (Badcock et al., 2005; Dickinson et al., 2009;
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Edwards & Badcock, 1995; Williams & Sekuler, 1984). With TAM signals, however, it is difficult to increase the number of elements without increasing the area of the annulus. Therefore, we instead used two complementary sets of conditions: one where the number of elements remained constant but the area of the annulus increased and a second where both the number of elements and the annulus area increased (see Figure 7). If observers are determining the global motion direction by monitoring a small region of space, thresholds should remain constant as long as the density of the array is constant. On the other hand, if observers are monitoring the entire array, thresholds will increase with increases in the size of the annulus and total number of elements.

2.8.1.1 Method and Procedure

In all the conditions, the size of the local Kanizsa elements was halved from the previous experiments so that each was contained within a 32’ x 32’ window. These were placed in annuli that varied in area (89, 175, 389, 430 square degrees). In the first level of conditions, there were 100 local TAM elements for all annulus sizes, thus the element density decreased with increasing annulus size. In the second level of conditions, the number of elements increased (100, 204, 312, 447) with increasing annulus size to maintain a constant element density. Coherence thresholds were estimated for seven conditions (the 89 square degrees annulus condition was the same for both levels) using the same SIFC adaptive staircase procedure used in Experiments 3 and 4, with 10 staircases conducted for all conditions in a counter-balanced order.
2.8.2 Results and Discussion

There was still clear pooling of TAM using the smaller Kanizsa elements with the annulus appearing to twist following shape change when coherence was high. Figure 8 shows coherence thresholds across the two conditions as a function of increasing annulus size. The pattern of results is the same across all three observers. When the number of elements was kept constant, thresholds increased with increasing annulus size. However, thresholds increased much more rapidly when the density of the array remained constant with increasing annulus size. To quantify this relationship, we fitted $\sqrt{N}$ (with $N$ being square degrees of visual angle) curves to the constant number level conditions with increasing annulus area. Note the same array for the constant number and constant density condition for the 89 square degrees condition is the same.
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to determine how area affects coherence thresholds. Figure 8 shows that these curves predict the thresholds for the constant number condition, suggesting that the area over which the signals are integrated itself acts as noise, interfering with detection of global TAM. On this reasoning, we then fitted $\sqrt{N^2}$ curves for the constant density condition, assuming that when both area and number of elements was increasing, it was likely the independent noise from each would summate causing a quadratic increase in threshold. Consistent with this logic, these curves provide a good fit for the coherence thresholds in the constant density conditions.

**Figure 8.** Thresholds for the three observers in Experiment 5 for increasing the size of the annulus in two conditions; one with 100 TAM elements always presented (constant number) or where the number of elements increased so that density was constant in all conditions. The continuous lines indicate the fitted $\sqrt{N}$ and $\sqrt{N^2}$ curves for the constant number and constant density levels of conditions respectively.

The additive effect of area and number of elements with increasing annulus size strongly indicates that observers were using signals across the entire annulus to determine motion direction. Our results, therefore, show the global TAM thresholds do not reflect merely monitoring a small region of the array, but instead reflect integration across the entire annulus. In turn, to use signals across the entire annulus area, observers would necessarily need to perceive multiple simultaneous instances of TAM (up to at least the 447 element arrays used here). These results, therefore, demonstrate that TAM
occurs without needing to attentively track each element; contrary to previous claims (Tse & Caplovitz, 2006; Tse et al., 1998), based on observations using only a single TAM element, that selective attention is needed in the parsing and matching steps that drive TAM. Our demonstration that multiple TAM elements can be simultaneously integrated provides empirical evidence that selective attentional engagement is not always necessary for the perception of TAM. It is also highly unlikely crowding explains these results as thresholds increased in the constant number condition with increasing eccentricities while there was decreasing density meaning that crowding was consistent or even decreasing (Nandy & Tjan, 2012). Considering the strong relationship we found between the results of the two conditions, it seems highly likely thresholds in the constant density condition increased because noise came from, as in the constant number condition, area combining with the addition elements presented in this condition. This explanation is, therefore, consistent with crowding not causing the increase in thresholds.

The result that both the number of local elements and the area itself that the elements are presented over act as noise is novel. Thresholds increased by $\sqrt{N}$ with increasing area size in the constant number condition and by $\sqrt{N^2}$ in the constant density condition when both number of elements and area increased. Previous studies in motion examined thresholds when increasing number of local elements in the same size annulus, thus increasing density, finding a $\sim\sqrt{N}$ increase (Badcock et al., 2005; Dickinson et al., 2009; Edwards & Badcock, 1995). But, no studies using conventional motion stimuli have yet systematically determined the relationship between both annulus area and number of elements on coherence thresholds. Our results are different from global form pooling as thresholds are constant when area increases with constant
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density, showing area does not act as noise (Dickinson et al., 2009). This suggests that global TAM pooling is not being treated as form information. The effect of both area and number of elements for TAM, therefore, present a novel finding for the global pooling of a motion stimulus. In future studies, it would be beneficial to establish the effect of area on conventional global motion pooling in order to determine whether TAM is being treated as like a motion stimulus.

2.9 General Discussion

2.9.1 Summary of the experiments

The present study demonstrates that multiple TAM elements can integrate into a coherent global percept. However, this global pooling was only observed after carefully controlling for motion energy as such signals easily override the high-level TAM pooling. This suggests that TAM is pooled by a separate system, with considerably less tolerance to noise, than the standard motion energy system. Control experiments showed that coherence thresholds cannot be explained by observers discriminating motion direction on the basis of static form cues which produced much higher thresholds. Our work also shows that global TAM pooling is not limited by observers selectively monitoring a small region of the annulus and instead reflects integration across a larger region. This is in contradiction to previous claims that selective attention is necessary for the perception of TAM with simpler stimulus displays (Tse et al., 1998).

2.9.2 Global form-motion interactions

The thresholds reported for all three types of global TAM motion were significantly higher than those for global dot motion, which are typically 5% to 15% (Baker et al., 1991; Edwards & Badcock, 1995; Newsome & Paré, 1988). Notably,
however, global dot motion coherence tasks need to consist of at least eight frames for asymptotic performance, suggesting that optimal global motion integration occurs over an extended period whereas thresholds are ~20% when only two frames are presented (Edwards & Badcock, 1995; Snowden & Braddick, 1989). This could explain the higher thresholds obtained for the Plunger and ILM arrays, which are pooled using motion energy, and consisted of only two frames. However, thresholds for the Kanizsa stimuli, which are pooled in a direction consistent with TAM, were also considerably higher than Plunger and ILM stimuli. One possible explanation is that global form-induced motion pooling integrates more weakly than that using motion energy inputs. Another option is suggested by Tse and Logothetis (2002) who argued that TAM objects are matched and parsed in each frame. It is possible that this process has less noise tolerance than simple spatiotemporal matching, thereby yielding higher thresholds. However, we think this explanation is unlikely as Experiment 5 showed thresholds decreased (as a proportion of total elements) when the number of elements in the same size annulus increased. A final possibility is that increased thresholds may have resulted from crowding, as the Kanizsa stimuli were more complex than the simpler Plunger and ILM stimuli.

Our finding that multiple Kanizsa TAM signals can be integrated provides additional insights into where form information can enter the motion system. There is considerable evidence showing V5/MT is necessary for global motion perception as this area shows greater responses to coherent than incoherent motion (Born & Yu, 2005; Kohn & Movshon, 2004; Smith et al., 1994), and disruptions to activity lead to reduced global motion sensitivity (Beckers & Hömberg, 1992; Beckers & Zeki, 1995; Newsome & Paré, 1988). Similarly, V3a also strongly responds to global motion stimuli (Braddick
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et al., 2000). Considered together with evidence that versions of TAM stimuli that do not control for motion energy seem to activate V5/MT (Tse, 2006; but see Bertrand et al., 2012), our results provide strong evidence that form information necessary for the TAM percept can enter the motion system by the level of V5/MT and/or V3a. This result is consistent with several different propositions about how form motion might reach V5/MT. For example, Grossberg and colleagues (Baloch & Grossberg, 1997; Francis & Grossberg, 1996) have argued for a form-motion ‘boundary completion wave’ emerging from activity in V2 that feeds into V5/MT. This model can account for the perception of TAM, including the Kanizsa stimuli used in the current study.

There is also substantial literature suggesting that V4 is central to global form perception as it integrates shape information across disparate orientations (Felleman & Van Essen, 1991; Gallant, Connor, Rakshit, Lewis, & Van Essen, 1996; Ungerleider, Galkin, Desimone, & Gattass, 2008). Furthermore, Kanizsa stimuli strongly activate both V2 and V4 while only weakly activating V1 (Lee & Nguyen, 2001; Pan et al., 2012). Joint consideration of these points opens up the possibility that extensive lateral cortical connections between V4 and V5/MT allow form information to provide an input for global processing in the motion system (Felleman & Van Essen, 1991; Maunsell & van Essen, 1983; Ungerleider et al., 2008). Alternatively, there is growing evidence that V4 itself is sensitive to motion, with a large number of direction sensitive cells within this area (Roe et al., 2012). This opens up the possibility that the TAM percept could also result directly from activation within V4. Although when considered in conjunction with the aforementioned results, it is likely that the global motion areas are also involved. As for V3a, globally-processed form information in TAM could have reached this area through its bilateral projections with V4 (Ungerleider et al., 2008). These results are also consistent with the finding that long-range apparent motion
causes activation in the ventral visual stream (Zhuo et al., 2003). V3a is responsive to moving shapes with contour curvature, showing the region is sensitive to form-motion interactions (Caplovitz & Tse, 2006). Tse et al. (2002) have previously shown that 3D processing of form information in TAM precedes the motion percept. Again this suggests a strong role of both V5 and V3a in global TAM pooling as these areas are strongly responsive to disparity cues necessary for 3D form perception (Adams & Zeki, 2001; Anzai, Chowdhury, & DeAngelis, 2011; Backus, Fleet, Parker, & Heeger, 2001).

It is also worthwhile to comment on likely differences between brain areas subserving TAM and biological motion. The later areas of the dorsal stream, superior temporal sulcus and superior temporal polysensory areas, have all been found to be central in the separate form-motion interaction of biological motion (Grossman & Blake, 2002; Vaina, Solomon, Chowdhury, Sinha, & Belliveau, 2001). Additionally, biological motion is still found in observers with bilateral lesions to the temporal lobes, who are unable to globally process form (Gilaie-Dotan, Bentin, Harel, Rees, & Saygin, 2011). This highlights what is likely a central difference between biological motion and TAM; TAM could not be perceived without global form processing because the form changes appear to drive the illusory percept.

2.9.3 Cross over between TAM and motion energy pooling

One of the most notable aspects of our results was the difference between global motion percepts generated by the Plunger and Kanisza TAM stimuli. Whereas the former showed global motion in the direction of motion energy, the latter did not. This dissociation suggests that the high-level filling-in process necessary for TAM breaks down when the Plunger stimuli are placed in the global array and the visual system reverts to low-level centroid tracking. One possible explanation for this lies in the fact
that the Plunger stimuli contain a stronger motion energy signal than the Kanizsa stimuli, as the centroid shift is approximately twice as large. To test this hypothesis, we constructed a modified version of the Kanizsa global array where the luminance of the elements was altered to produce a larger centroid shift in the direction opposite to TAM (Movie 6). This modification diminished the perceived global rotation in the direction of TAM following the shape changes although unlike the Plungers, the motion direction was not reversed. We attempted to collect global motion thresholds using an adaptive staircase procedure for this stimulus. However, observers could no longer reliably judge the motion direction, even with very high coherence levels. This suggests that increasing low-level motion energy simply swamped the processes underlying the global motion percept. When taken in conjunction with our previous results, it provides additional evidence that the motion energy system overrides the TAM system when motion energy cues are sufficiently strong.

Movie 6. The modified version of the Kanizsa global TAM array with a greater centroid shift. The luminance of the two Pacman in the direction opposite TAM motion increases in the second frame of the sequence. This causes the stimuli to have a similar motion energy signature as the Plunger stimulus. Observers could no longer complete a coherence task when this stimulus was placed in a staircase procedure, suggesting that the illusory motion has been greatly diminished.

The relationship between global TAM pooling and motion energy suggests a
possible functional role for form changes during optic flow. If an observer is continually fixating forward in an optic flow situation then the appearance of shapes on the retina will morph with the relative motion of the observer. The ability for multiple TAM signals to integrate suggests that the visual system could use the information from form changes during optic flow to help ascertain motion direction. However, as we found that the motion energy relatively easily overwhelms global TAM pooling, it appears that the visual system has a preference for motion energy signals over motion information derived from form changes. Furthermore, the results from Experiment 5 show TAM thresholds dramatically increase with increasing number of elements in the arrays, far more so than conventional motion stimuli. This suggests that the motion system may not be optimized for integrating information derived from shape changes.

### 2.9.4 Conclusions

Overall, the current results show that multiple TAM signals can integrate to create a global perception of motion, although this can only be seen after carefully controlling for motion energy. A separate global system appears to be involved in global TAM pooling that shows a much lower tolerance to noise than the conventional motion energy system driven. This is possibly due to the complexity of the stimuli, or because the motion information is form driven which requires a greater signal level. Furthermore, we showed that observers were integrating local TAM signals across the entire array and, therefore, simultaneously perceived multiple TAM signals, indicating that selective attention is not necessary for TAM motion to be perceived.
2.10 References


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3 The broad orientation dependence of the motion streak aftereffect reveals interactions between form and motion neurons


School of Psychology, The University of Western Australia, Crawley, Western Australia, 6009, Australia.

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3.1 Foreword

Traditional theories of visual perception have argued that form and motion information are processed in separate neural pathways. A widely-used model argues that motion direction follows the motion energy of a moving object (Adelson and Bergen, 1985). This model can explain many existing motion phenomena and appears to give a reasonably successful account of low-level motion processing. But there is now, however, growing evidence showing that form and motion processes do indeed interact, contrary to the traditional assertions. Transformational apparent motion (TAM) clearly demonstrates that form and motion interact in a way unpredicted from the dominant motion processing models. In certain stimulus configurations, TAM leads to the perception of motion in the direction opposite to low-level motion energy predictions.

There was uncertainty about the level at which the interaction between form and motion that drives the percept of TAM arises. Chapter 2 (Tang, Dickinson, Visser, Edwards and Badcock, 2013) showed that the form-driven motion percept generated by a TAM display enters the motion system by, at least, the stage of global motion pooling. However, TAM does appear to be easily overcome by low-level motion energy as evidenced by the perceived motion direction following motion energy, not TAM, predictions when multiple local ‘plunger’ elements were presented. Therefore, form information inputs into the motion system by, at least, the stage of pooling but its interaction with motion energy is uncertain. It is, however, possible that the form information is able to enter the motion system earlier than the stage of global motion pooling.
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One influential model argues that form and motion interact at V1 (Geisler, 1999). The model argues that the extended integration time of V1 neurons causes the neural equivalent of orientation cues along the axis of motion. The model states that these ‘motion streaks’ are multiplicatively combined with the motion signals from the object in V1. This combination process causes motion signals to have the fidelity of form information. While there have been a number of studies which have confirmed that fast translational motion causes form-like responses in early visual areas, no study has yet provided a comprehensive test of the motion streaks model, including whether streak-causing motion signals are processed like form information. If this model is correct, then form information enters the motion system at V1 and changes how motion signals are processed. It is, therefore, possible that this mechanism could account for our previous results showing that TAM enters the motion system by, at least, the stage of global motion integration. The current study aims to provide a comprehensive test of the model to determine at what stage form information is entering the motion system.

References


3.2 Abstract

The extended integration time of visual neurons can lead to the production of the neural equivalent of an orientation cue along the axis of motion in response to fast-moving objects. The dominant model argues that these ‘motion streaks’ resolve the inherent directional uncertainty arising from the small size of receptive fields in V1, by combining spatial orientation with motion signals in V1. This model was tested in humans using visual aftereffects, where adapting to a static grating causes the perceived direction of a subsequently-presented motion stimulus to be tilted away from the adapting orientation. We found that a much broader range of orientations produced aftereffects than predicted by the current model, suggesting that these orientation cues influence motion perception at a later stage than V1. We also found that varying the spatial frequency of the adaptor changed the aftereffect from repulsive to attractive for motion-test, but not form-test stimuli. Finally, manipulations of V1 excitability, using transcranial stimulation, reduced the aftereffect, suggesting that the orientation cue is dependent upon V1. These results can be accounted for if the orientation information from the motion streak, gathered in V1, enters the motion system at a later stage of motion processing, most likely V5. A computational model of motion direction is presented incorporating gain modifications of broadly-tuned motion-selective neurons by narrowly-tuned orientation-selective cells in V1, which successfully accounts for the extant data. These results reinforce the suggestion that orientation places strong constraints on motion processing, but in a previously undescribed manner.
3.3 Introduction

How neurons in V1 signal the direction of object motion has been a dominant question in visual neuroscience. An aperture problem arises as the small receptive fields of V1 neurons make elongated contours produce ambiguous motion direction estimates (Adelson & Movshon, 1982). While pooling multiple signals in higher visual areas can solve this problem (Adelson & Bergen, 1985; Amano, Edwards, Badcock, & Nishida, 2009a), an alternative solution uses the extended integration time of V1 neurons, which causes fast-moving objects to create the neural equivalent response of a spatially-extended form cue along the axis of motion (Badcock & Dickinson, 2009; Geisler, 1999; Geisler, Albrecht, Crane, & Stern, 2001). Geisler suggested that multiplicatively combining these ‘motion streaks’ with motion signals, in V1, gives motion the directional precision of form information. Consistent with this suggestion, presenting a rapid succession of locally-uncorrelated patterns with a consistent global pattern results in perception of motion in the global pattern direction (Ross, Badcock, & Hayes, 2000). Additionally, motion streaks have been shown to increase sensitivity to global motion and influence perceived motion direction (Apthorp et al., 2013; Burr & Ross, 2002; Edwards & Crane, 2007). There has been evidence showing that fast translational motion leaves an orientation cue (a motion streak) parallel to the motion axis (Apthorp & Alais, 2009; Apthorp, Cass, & Alais, 2010; Apthorp, Cass, & Alais, 2011; Apthorp et al., 2013; Apthorp, Wenderoth, & Alais, 2009; Geisler et al., 2001), but a critical test about how this streak is combined with motion direction information has yet to be reported.

Visual aftereffects have been used for many years to non-invasively estimate system properties underlying human perception. The tuning of the orientation mechanisms in V1 has been shown using the tilt aftereffect (TAE; Clifford, 2002,
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2014), where adapting to static features causes the perceived orientation of subsequently-presented features to be tilted away from the adapted orientation. This effect is dependent on the orientation difference between adaptor and test, with the magnitude of repulsion peaking for separations of 15-20°, then declining at larger separations and finally yielding a small attractive aftereffect at separations near 75° (Clifford, 2002; Gibson & Radner, 1937; Wenderoth & Johnstone, 1988). This roughly corresponds with neurophysiological evidence showing that the response of orientation-selective neurons is biased away from the adapted orientation for nearby but not distant orientations (Figure 1a-c) (Dragoi, Sharma, & Sur, 2000) and supports the angular dependence of the TAE being consistent with the orientation bandwidth of V1 neurons (full width at half maximum (FWHM) 40°) (K. K. De Valois, 1977). Notably, however, the angular dependence of motion-direction aftereffects peaks between 30-40° (Schrater & Simoncelli, 1998), consistent with the bandwidth of motion-sensitive neurons in V5 (FWHM ~90°) (Albright, 1984; Snowden, Treue, & Andersen, 1992), but not the 180° bandwidth of motion-sensitive neurons in V1 (Movshon, Adelson, Gizi, & Newsome, 1985).
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**Figure 1.** a-c. A hypothetical example showing how changing neuronal response can account for the TAE using a channel-based model of orientation coding. This example also shows why measuring the angular dependency of the aftereffect estimates the underlying bandwidth of the neuronal population. a. The seven orientation channels are equally responsive before adaptation to their preferred orientations. The population response is centered at 10° when a stimulus with a 10° orientation is presented prior to adaptation (red curve). b. The channels selective for the adapted orientation (0°) are maximally depressed following adaptation at this orientation. When a stimulus with a 10° orientation is again presented following adaptation, the combined population response shifts away from the veridical orientation. c. The magnitude of the aftereffect depends on the relationship between the test stimuli’s orientation and bandwidth of the adapted neurons. The blue line indicates predicted aftereffect for the indicated adaptor orientations with narrowly-tuned neurons whereas the yellow line indicates the aftereffects with broadly-tuned neurons. d. Simplified versions of the stimuli used in the motion and form test conditions in the experiment. The arrows indicate the direction of travel for each dot across the four stimulus frames for the motion stimuli. e. A schematic representation of the trial.

We examined the motion-streak mechanism using a static adaptor to change the perceived direction of motion or orientation of static form stimuli (Movie 1).
angular dependence of the motion direction aftereffect was twice as broad as form and
differently modulated by adaptor spatial frequency, suggesting the orientation and
motion signals are combined at a later stage of motion pooling, not V1. Using
transcranial direct current stimulation (tDCS) to increase the excitability of V1 reduced
the aftereffect suggesting orientation information is inherited from this area. A new
model for motion direction is provided where narrowly-tuned orientation-selective
neurons modulate broadly-tuned motion-selective neurons at a different processing
stage.

**Movie 1.** The motion streak aftereffect; the perceived direction of vertical global dot motion appears
repelled away from the orientation (30°) of the static adapting Gabor.

### 3.4 Methods

#### 3.4.1 Observers

Four observers (3 males), between 22 and 49 years (median = 25 years), took
part in all experiments. Authors MFT and JED participated while the other observers
were naïve to the experimental aims. These observers were extensively tested, the data
presented here required 89,600 trials taking approximately 100 hr to collect. The
extensive testing and fully-within subjects design, with each acting to replicate the
effects, allowed us to be very certain of each observer’s performance. There was very
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little variation reported between the different observers. All observers had normal or corrected-to-normal visual acuity as measured using a LogMAR chart. The procedure was in accordance with the Declaration of Helsinki and approved by the Human Research Ethics Committee at the University of Western Australia with all observers providing written, informed consent.

3.4.2 Apparatus

The stimuli were generated in MATLAB 7.14 on a MacBook Pro (i7, 2.53 GHz) with a NVIDIA GT330M graphics card using PsychToolbox. The stimuli were displayed on a Sony Trinitron G520 monitor with a 120 Hz refresh rate at a resolution of 1024 × 786 pixels using a Cambridge Research System Bits# system to achieve 14-bit gray scale resolution. Observers viewed the monitor from 70 cm (maintained with chin rest) resulting in the display subtending 31° × 23° (pixel subtense of 1.8’ × 1.8’). The luminance was gamma-corrected using a Cambridge Research System ColorCAL II and custom-written software. The background display luminance was 80 cd/m² with a maximum of 160 cd/m².

3.4.3 Stimulus and psychophysical procedure

Test stimulus. Global dot motion was used as the motion stimulus, with all 100 dots having Gaussian luminance profiles and translating coherently (Movie 1). The maximum luminance of a dot was 160 cd/m² and the minimum was 80 cd/m². The diameter of the dots was 0.33°, equating to four times the standard deviation of the Gaussian luminance distribution. Each dot was randomly positioned within a 10° circular aperture at the beginning of each trial. All dots then translated at 10°/s, for 4 stimulus frames (unless otherwise noted), with each frame presented for 3 refreshes of the monitor (an effective animation rate of 40 Hz), in a consistent global direction. A
dot wrapped around the aperture, reappearing on the opposite side, if it was going to move outside the aperture on the next frame. A number of control conditions (described below) were run to evaluate the influence of low-level image properties. The stimuli in the form conditions (Movie 2) were the same as the motion stimuli but the dots in the 4 frames were added all to the same frame and presented simultaneously giving the impression of at least 100 oriented lines (depending on the wrapping).

**Movie 2.** The static tilt aftereffect, which was used for the form-test condition. Similarity to Movie 1, the perceived orientation of the field of lines appears tilted away from the orientation (15°) of the adapting Gabor.

**Procedure.** Each trial began with a central fixation dot (Figure 1e). An oriented adapting Gabor (a sinusoidal grating modulated by a 2D Gaussian window) with an envelope standard deviation of 1.66° was then presented. The spatial frequency of the adapting Gabor was 3 c/°, unless otherwise noted. On each trial, an adaptor was presented for 3 s followed by a 160 ms inter-stimulus interval before the 100 ms test stimulus was presented (Figure 1c). Observers then indicated whether the test stimulus’s direction or orientation was to the left or right of vertical using a keyboard. Stimuli were centered 9° to the right of fixation as peripheral presentation increases the magnitude of the aftereffect without affecting its reported angular dependence (Dickinson, Harman,
Tan, Almeida, & Badcock, 2012; Muir & Over, 1970) suggesting that there is no effect on angular dependence for using peripheral presentation.

The aftereffect was estimated by measuring magnitude of direction or orientation repulsion from vertical (depending on the condition) after adapting to an oriented Gabor. The aftereffect’s orientation dependence was estimated by varying the orientation of the adapting Gabor (-90°, -70°, -50°, -30°, -20°, 0°, 20°, 40°, 60°, 80°) from vertical in separate blocks of trials. The method of constant stimuli was used to vary the true direction or orientation of the test stimulus with 40 trials presented for each of the seven directions in a pseudo-randomized manner. The order of adapting orientations tested was also pseudo-randomized between the observers. The range of angular deviations of the motion direction or form orientation used for the method of constant stimuli steps was adapted for each observer in order to measure their entire psychometric function.

3.4.4 Data analysis

The probability of the observer reporting that the test stimulus orientation or direction was to the right of vertical was calculated for each stimulus direction or orientation. Cumulative Gaussian functions were fitted to these responses in each condition, with the mean indicating the point of subjective equality (i.e., the true direction or orientation the stimuli needs to vary from vertical to be perceived vertical after adaptation). The points of subjective equality for all adaptor orientations were fitted using the first derivative of a Gaussian (D1, Eqn. 1), to measure the angular dependence of the aftereffects. All fitting was done using non-linear regression in GraphPad Prism (6.0c for Mac, GraphPad Software, CA, USA) which gives parameter estimates and associated 95% confidence intervals based on the precision of the model fit.
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\[ D_1 = A \times \frac{1}{\sigma} \times \theta \times \exp\left(-\frac{\theta^2}{2\sigma^2}\right) + C \]

*Equation 1.* $A$ is a free parameter representing the amplitude of the curve. $\sigma$ is a free parameter representing the width of the function. $\theta$ is the physical orientation of the adapting Gabor. $C$ is also a free parameter for a constant offset to correct for any systematic response biases.

### 3.4.5 tDCS procedure

Transcranial stimulation was delivered using a constant-current battery-driven stimulator (Dupel Iontophoresis System, MN) through two $6 \times 4$ cm saline-soaked electrodes placed in pouches on the scalp. The active electrode was placed directly above the mastoid bone while the reference was placed at position Cz in the International 10-20 System (Homan, Herman, & Purdy, 1987). Both electrodes were aligned along the midline. This montage has previously been shown to increase excitability of the visual cortex with anodal stimulation and decrease excitability with cathodal stimulation, as measured by changes in the early visual component N70 visual evoked potential (Accornero, Li Voti, La Riccia, & Gregori, 2007). The polarity of the electrode placed above the mastoid bone defines the type of stimulation. The current was gradually increased over 30 s to 2 mA at the start of the session then maintained at this level until the end of testing where it was decreased to 0 mA over 30 s.

Psychophysical procedures began 30-60 s after the start of stimulation. Previous work suggests there is no difference in sensation between anodal and cathodal stimulation meaning that observers were effectively blind to the condition (Tadini et al., 2011). The authors were also blind to stimulation condition until completion of testing as another experimenter conducted the experiment.
3.5 Results and discussion

3.5.1 The motion streak aftereffect shows broader angular dependence than the TAE

We began by measuring the angular dependence of the motion streak mechanism by examining how the orientation of an adapting static grating alters the perceived direction of subsequently-presented motion. This was compared to the conventional TAE measured using static adaptors and test stimuli. Geisler (1999) showed that adapting to a static orientation repels the perceived direction of subsequently presented motion. He did not, however, measure the angular dependence of this aftereffect, nor compare it to the TAE, and thus could not determine whether this mechanism has the properties of a narrowly-tuned form (which Geisler’s model predicts) or a broadly-tuned motion system. To address this question, the angular dependence for motion streak test stimuli was compared to that for static versions of the test stimuli in order to compare the tuning of the motion streak mechanism to that of the static-form angular dependence.

Figure 2 shows the magnitude of the aftereffect plotted against the adaptor orientation. The normal TAE was obtained in the form-test condition with the orientation of the stimuli repelled away from the adaptor, with maximum repulsion occurring when the adaptor was oriented around 20° from vertical (Clifford, 2002; Clifford, Wenderoth, & Spehar, 2000; Dickinson, Almeida, Bell, & Badcock, 2010; Dickinson et al., 2012; Gibson & Radner, 1937; O'Toole & Wenderoth, 1977). The perceived motion direction was repelled away from the direction of the adapting orientation in the motion-test condition, showing the static-induced direction-aftereffect (SI-DAE). The maximum direction repulsion, however, occurred when the adaptor was around 40° from vertical, which is similar to the angular dependence previously
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reported in the direction aftereffect (Kohn & Movshon, 2004; Levinson & Sekuler, 1976; Schrater & Simoncelli, 1998), and double that found in the same observers in the form-only condition.

Figure 2. a. The magnitude of the aftereffect measured using motion (SI-DAE) and static (TAE) dot test stimuli following adaptation to static Gabors of various orientations (n = 4). A positive value of the adaptor orientation indicates the grating is rotated anti-clockwise from vertical, while positive indicates clockwise rotation. The fitted function is a first derivative of a Gaussian (D1). The error bars represent ±1 standard error. b. The average angular dependence (sigma values of the fitted D1 function) across observers for the fitted D1 curves for the two conditions. The error bars represent within-subjects ±1 standard error.

D1 functions (Eqn. 1) fitted to each observer’s data yield a σ value that estimates the angular dependence of the aftereffect. A paired-samples t-test comparing σ for the motion and form-test conditions shows the motion-test condition was broader than in the form-test condition, t(3) = 8.04, p = .004, $R^2 = .96$. This suggests that the
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presence of a motion streak does not cause motion to be processed entirely by the same set of orientation-tuned mechanisms as form stimuli as predicted by Geisler (1999). The model would predict a narrower range of orientations causing aftereffects, and the results suggest that orientation is only affecting perceived motion direction at a later stage of the processing hierarchy. The angular dependence is consistent with the direction aftereffect and the broad bandwidths of motion-selective neurons in V5 (Albright, 1984; Britten & Newsome, 1998; Rodman & Albright, 1987; Snowden et al., 1992) as a full-width at half-height bandwidth measurement of 90°, which is often reported for MT neurons, is equivalent to a 40° width of the Gaussian-derivative function we fitted to the data (mean $\sigma = 38.82$, 95% CI = 35.43-42.20).

3.5.2 Controlling for low-level image properties

We will now report a number of control experiments that showed that the broader angular dependence for the motion stimulus was due to properties of mechanism tuning rather than the low-level properties of the stimuli. In the first two control conditions (half form and half motion), we increased the range of orientation content of the test stimuli by 50% (Figure 3c-e). See Figure 3 for detailed explanation. These conditions were the same as the previous task but only 2 frames were presented yielding shorter, less-precisely oriented form or motion signals. The behaviorally measured angular dependence for the half-form condition was similar to the full-form condition; likewise, angular dependence did not vary between the half- and full-motion conditions (Figure 3). A paired-samples t-test failed to find a difference in $\sigma$ between the full- (mean $\sigma = 39.59$, 95% CI = 33.34-45.78) and half-motion (mean $\sigma = 36.32$, 95% CI = 33.64-38.99) condition, $t(2) = 1.63$, $p = .25$, $R^2 = .57$. Likewise, the tuning function of the full- (mean $\sigma = 20.80$, 95% CI = 18.98-22.61) and half-form (mean $\sigma =$}
25.23, 95% CI = 22.46-27.99) conditions were similar although statistically significantly different, \( t(2) = 9.59, p = .01, R^2 = .98 \). This shows that under these conditions these functions are not limited by the intrinsic orientation uncertainty in the stimulus as smearing the orientation information over a broader range in the half motion and form conditions did not alter the angular dependence of the aftereffects by equivalent amounts. This suggests that the orientation uncertainty in the stimuli were less than that in the mechanisms detecting the orientation/direction, meaning that the measured angular dependence is not caused by stimulus-specific parameters.
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**Figure 3.**

**a.** The magnitude of the aftereffects plotted against the adaptor orientations in the control conditions with the half form (TAE) and half motion (SI-DAE) stimulus (n = 3). The error bars indicate ±1 standard error.

**b.** The mean sigma values of the fitted D1 functions for these conditions compared to the sigma values in the original experiment. The error bars represent within-subjects ±1 standard error.

**c-d.** Gaussian-dots stimuli with dot repetitions of one (c), two (d) or four (e), plotting the two-dimensional Fourier spectrum in the left column and a corresponding example of the stimulus in the right. The frequency response for the stimuli was taken from the average Fourier spectrum of 2500 iterations of each stimulus type (to control for the randomization of each stimulus in the experiment. The orientation spectrum becomes elongated as more dots are added to the line segments, showing that the energy in the orientation spectrum is more concentrated on the direction of elongation in the full- than half-form condition. This was confirmed when we took the full-width at half-height measurements for response to vertical orientation across conditions. The full-form condition (10.35°) having a much narrower orientation spectrum than the half-form condition (15.35°).

A further control condition examined whether the spatial frequency profile of the test stimuli affected the measured angular dependence of the SI-DAE. This experiment was motivated by the finding that orientation selectivity of V1 neurons in
macaque becomes increasingly narrow with higher spatial frequency stimuli (R. L. De Valois, Albrecht, & Thorell, 1982). The spatial frequency content of the stimuli may explain the different orientation dependencies of the form and motion-test stimuli because the dots had a Gaussian profile with a small sigma and therefore a broad spatial frequency profile (Figure 4a-c). To test this option, we measured the angular dependence of the SI-DAE using dots with a luminance profile of a fourth derivative of a Gaussian (D4), which changed the peak spatial frequency from 0 c/° to 7.3 c/°. We also changed the spatial frequency of the adaptor to 7.3 c/° to coincide with the spatial frequency of the dots. Results obtained with this modified procedure were similar to the initial experiment. A paired samples t-test showed the σ values between the Gaussian- and D4 test-motion conditions were not significantly different, $t(2) = 1.47, p = .28, R^2 = .51$. Taken together, these control experiments demonstrate that the angular dependence of the SI-DAE was not due to these stimulus-specific attributes and, instead, suggests the results reflect mechanism tuning.
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Figure 4. a. An enlarged version of the dots used in the D4 condition. b. The luminance profile of a horizontal slice through the middle of the D4 dot compared to the normal Gaussian dot. c. The spatial frequency profile of the D4 dot, the peak spatial frequency occurred at 7.5 c/°, compared to the Gaussian dot, the peak spatial frequency occurs at 0 c/°. d. The magnitude of the aftereffect for the D4 (blue line) and Gaussian (red line) dots plotted against the orientation of the adaptor (n = 2). The error bars indicate ±1 standard error. e. A summary graph of the sigma values of the fitted functions for the observers. The error bars represent within-subjects ±1 standard error.

3.5.3 Orientation and motion selective neurons have a reciprocal relationship

In a previous study, Apthorp and Alais (2009) argued that adapting to streak-inducing motion leads to a TAE with similar angular-dependence to the standard TAE. Importantly, however, they drew this conclusion by comparing their results to previous reports of the TAE gathered from different subjects using different stimuli. In order to ensure direct comparability, we used a within-subjects design to re-examine the impact of streak-induced motion on the TAE. To do this, we reversed the stimulus types from...
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the first experiment with observers adapting to 3 s of fast-moving translational motion that varied in direction followed by a test static Gabor stimulus that was oriented around vertical. The direction of the adapting motion was varied across blocks to sample the entire direction-orientation function.

Adapting to oriented motion direction caused a small change in the perceived orientation of the static-test Gabor away from the adaptor direction (Figure 5). The magnitude of this aftereffect was slightly smaller than that reported by Apthorp and Alais (2009). This is likely due to the shorter adaptation time used in the current study, which has an inverse exponential relationship with the magnitude of the aftereffect (Greenlee & Magnussen, 1987; Magnussen & Johnsen, 1986). The smaller magnitude of the aftereffects, however, should have little effect on the measured angular dependence (Dickinson et al., 2012).
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Figure 5. The effects of adapting to motion on the perceived orientation of subsequently-presented static Gabors. a. The magnitude of the TAE plotted against the direction of the adapting motion direction (n = 4). The error bars indicate ±1 standard error. b. A summary graph of the sigma values of the fitted functions for the observers. The error bars indicate within-subject ±1 standard error.

The angular dependence was broader than for the form-adapt and form-test condition, but slightly narrower for the SI-DAE measured in the previous experiments. As the angular dependence of this aftereffect was somewhere between the motion-test and form-test condition, it suggests that the motion streaks are adapting narrowly-tuned orientation-selective neurons in addition to the broad influence of motion neurons exerting gain on orientation. In the modeling section, we show that the angular dependence in this condition can be accounted for by broadly-tuned motion-selective neurons modulating the gain of narrowly-tuned orientation-selective neurons, with the presence of the motion streak also causing additional adaptation of orientation-selective
neurons. This result suggests motion-selective neurons in V5 may reciprocally influence orientation-selective neurons in V1.

These results also rule out a possibility that the form and motion test stimuli after adapting to static form are activating different populations of V1 neurons. It is possible that the motion-test stimuli activate neurons perpendicular to the motion axis and neurons parallel to the motion axis because of the motion streak. The form-test stimulus, however, may only be activating neurons parallel to the orientation, as the test stimulus does not move. It is, therefore, possible that motion-test stimuli are activating a broader range of neurons than activated by the form-test stimuli. However, the results for the motion-adapt condition suggest this is not the case. If the motion stimuli were activating both parallel- and perpendicularly-oriented neurons then the D1 function would be a poor fit to the aftereffects, as sizable aftereffects would emerge at very large adaptor directions (±75-90°). Contrary to this prediction, this function provided a very good fit to the data (mean $R^2 = .84$, $SD = .04$).

### 3.5.4 Spatial frequency selectivity of SI-DAE

The static TAE is selective for spatial frequency, with the greatest aftereffect occurring when both test and adaptor stimuli have the same spatial frequency and decreasing as the difference in spatial frequency of adaptor and test increases. The aftereffect disappears when there is more than one octave difference in spatial frequency between the adaptor and test (Ware & Mitchell, 1974). These behavioral findings are consistent with neurophysiological measurements of spatial frequency selectivity of neurons in V1 (R. L. De Valois, William Yund, & Hepler, 1982). On the other hand, global motion integrates across spatial frequency, consistent with the neurophysiological findings that V5 neurons are broadly tuned for spatial frequency.
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(Amano, Edwards, Badcock, & Nishida, 2009b; Bex & Dakin, 2002; Movshon & Newsome, 1996; Simoncelli & Heeger, 1998). The broad angular dependence of the motion streak aftereffect suggests the aftereffect is dependent on the stage of global motion pooling, most likely at V5. On this logic, the SI-DAE would be predicted to show a different spatial frequency dependency compared to the static TAE. To test this prediction, we examined the effect of varying the spatial frequency of the adaptor on the magnitude of the SI-DAE and TAE. The same procedures were used as in the first experiment, but with the magnitude of the aftereffect measured with one adaptor orientation (20°), which varied in spatial frequency.

We replicated the spatial-frequency specificity of the TAE in the form condition with the aftereffect being largest when the adaptor was 1-4 c/° and reduced when the adaptor had a lower or higher spatial frequency than this, finally disappearing at higher spatial frequencies (Figure 6). The effective spatial frequency of the form dots may have resulted in this spatial frequency tuning because of the observer's contrast sensitivity for a Gaussian dot. This can be given by multiplying the typical contrast sensitivity at 10 Hz (Robson, 1966), the presentation rate of the test stimuli, with the spatial frequency spectrum of the Gaussian dot (Figure 4c). This manipulation means the function peaks at 0-4 c/° before reducing to zero at the higher spatial frequencies. A masking study found similar spatial frequency tuning for streak-inducing Gaussian dots with similar properties (Apthorp et al., 2011).
Figure 6. The magnitude of the motion- (SI-DAE) and form-test (TAE) following adaptation to a Gabor with a 20° orientation (n = 4) as a function of spatial frequency. Response bias was removed from each observer’s results by the constant offset value measured in the first experiment. Error bars indicate ±1 standard error.

Most importantly and surprisingly, in the motion condition the SI-DAE went from repulsive to attractive when the spatial frequency of the adaptor was changed. We believe this arises because of the increased contrast sensitivity that occurs when the adaptor and test are separated by more than two octaves of spatial frequency (K. K. De Valois, 1977). This explanation is consistent with the orientation information from the motion streak first affecting the perceived motion direction at the level of global motion processing, most likely V5, which receives inputs from a broad range of spatial frequencies, rather than V1 which is selective for a narrow range of spatial frequencies (Movshon & Newsome, 1996).

This attractive effect can be explained if it is assumed that sensitivity is decreased by adaptation for nearby spatial frequencies, but *increased* when there are
more than two octaves of difference following adaptation (Blakemore & Campbell, 1969; K. K. De Valois, 1977; Greenlee & Magnussen, 1988). Interactions between neighboring V1 neurons with different spatial frequencies is thought to cause spatial frequency-dependent changes (both excitatory and inhibitory) of contrast sensitivity with adaptation (K. K. De Valois, 1977). Changing from inhibitory response at the same spatial frequency to an excitatory response at different spatial frequencies can, thus, explain the change from repulsive to attractive aftereffects.

This attractive aftereffect is particularly interesting because in the TAE perceived orientation is not attracted following adaptation to gratings with different spatial frequencies (Carandini & Ferster, 1997; Dickinson & Badcock, 2013; Ware & Mitchell, 1974). Perceived orientation can, however, exhibit spatial-frequency dependent attraction and repulsion during simultaneous, rather than sequential, presentation which can be accounted for by the same change from inhibitory to excitatory gain modulation (Dickinson et al., 2012; Skillen, Whitaker, Popple, & McGraw, 2002). The difference between the SI-DAE and the TAE may be due to the broad spatial frequency tuning of V5 as the inputs from separate spatial frequencies would influence the same motion representation (Bex & Dakin, 2002; Movshon & Newsome, 1996; Simoncelli & Heeger, 1998), compared to the narrow spatial frequency tuning in V1 (R. L. De Valois, William Yund, et al., 1982), where the TAE is generally thought to arise (Fang, Murray, Kersten, & He, 2005).

The unexpected change from a repulsive to attractive aftereffect motivated us to measure the full orientation function for the attractive SI-DAE to further investigate its origins. To do this, the same procedure was used as in the first experiment but the spatial frequency of the adaptor was changed from 3 c/° to 1 c/°, as adapting to a 1 c/° static Gabor caused a large attractive aftereffect in the previous experiment. The
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Attractive effect occurs for all tested adaptor orientations with the magnitude of the effect peaking when the adaptor orientation was ~35° from vertical (Figure 7). This is similar to the width of the function we found in the first experiment for a repulsive aftereffect with a 3 c/° adaptor suggesting they may be represented in the same set of broadly-tuned neurons. As our attractive aftereffects are well-described by the first derivative of a Gaussian (D1) function, it is reasonable to suggest that the same channel-based mechanism could be responsible for both the attractive and repulsive effects, as we will show in our model below.

![Adaptor Orientation (°) vs. SI-DAE (°)](image)

**Figure 7.** The magnitude of the SI-DAE as a function of the orientation of an adapting 1 c/° Gabor (n = 3), showing an attractive aftereffect. Error bars indicate ±1 standard error.

### 3.5.5 Increasing excitability of V1 reduces the magnitude of the SI-DAE

The results from the previous experiments strongly suggest the orientation information from motion streaks influences motion direction processing at the stage of global motion pooling, most likely V5. This is contrary to the currently dominant model that argues solely for the involvement of V1. To further investigate the involvement of V1 in our effects, we used transcranial direct current stimulation (tDCS), a non-invasive technique, to alter cortical excitability. Anodal tDCS increases and cathodal tDCS
decreases excitability by altering the resting membrane potential of the stimulated neurons (Nitsche et al., 2003; Stagg & Nitsche, 2011), as shown by concomitant changes in corticospinal excitability (Nitsche et al., 2003; Nitsche & Paulus, 2000) and hemodynamic response (Lang, Nitsche, Paulus, Rothwell, & Lemon, 2004).

Stimulation over the occipital pole alters early components of the visual evoked potential (Accornero et al., 2007) and shows polarity-dependent modulation of V1 excitability (Antal, Kincses, Nitsche, & Paulus, 2003). The effect of tDCS applied over visual cortex appears to be relatively specific to the location of stimulation with neuroimaging showing that stimulating V5 increases excitability in this area but not V1 (Antal et al., 2012). This is mirrored by behavioral results with learning on a motion task improved when stimulation was delivered to V5, but not when delivered to V1 (Antal, Nitsche, et al., 2004) and the duration of motion aftereffects is only reduced when stimulation is delivered over V5 with no corresponding effect when delivered over V1 (Antal, Varga, et al., 2004). It, thus, appears likely that excitability changes are relatively localized at the targeted stimulation site.

We examined the effect of applying tDCS over V1 on the SI-DAE to determine whether this area is involved in the aftereffect (Figure 8). A one-way repeated-measures ANOVA revealed significant effects of stimulation condition on the magnitude of the SI-DAE, \( F(2,11) = 6.22, p = .034, R^2 = .67 \). Post-hoc comparisons with Bonferroni’s correction indicated that anodal tDCS reduced the magnitude of the aftereffect compared to the baseline condition (adjusted \( p < .05 \)) but there was no difference between the cathodal and baseline conditions (adjusted \( p > .05 \)). This result supports previous studies showing that motion streaks are formed in early visual areas (Apthorp & Alais, 2009; Apthorp et al., 2013; Geisler et al., 2001). Adapting to an oriented feature causes orientation-specific hyperpolarization of neurons in V1 (Carandini &
Ferster, 1997), which leads to the TAE through a reduction in contrast sensitivity to nearby orientations (Blakemore & Campbell, 1969; Clifford, 2014). We hypothesize that the reduction of the aftereffect with anodal tDCS may be because increasing the excitability of neurons in V1 reduces the hyperpolarization of the oriented channels during adaptation. This, in turn, suggests that early visual cortical areas are involved in the aftereffect, in addition to later processing stages already identified in our previous experiments.

Figure 8. The group magnitude of the SI-DAE during anodal and cathodal tDCS stimulation compared to baseline performance (n = 4). The error bars indicate within-subject ±1 standard error.

3.5.6 An alternative model of motion streak input to motion perception

Geisler’s (1999) original model of motion streak processing posited that form information, detected by orientation-selective neurons, is multiplicatively combined with motion-sensitive information in V1. This combination results in direction information having the precision of spatial information (Geisler, 1999; Geisler et al., 2001). Our results, however, suggest that this model needs to be reconsidered because the angular dependence of motion streak aftereffects are similar to motion signals
measured using test stimuli (gratings and plaids) that would not produce motion streaks (Schrater & Simoncelli, 1998) and double that of the angular dependence for orientation. The spatial frequency dependency of the aftereffect also suggests that orientation is affecting the stage of global motion integration. An alternative model can describe these results using narrowly-tuned orientation-selective neurons feeding either inhibitory or excitatory gain to a separate population of more broadly-tuned direction-selective neurons at a later stage of the processing hierarchy. Figure 9a shows a schematic representation of this proposed model of motion streak processing. Rather than providing a comprehensive account of the visual processing, we hope to show with a simple algorithmic model that orientation can affect motion direction processing which will account for our observed pattern of results. In this regard, the model is complimentary to existing theories of motion processing (i.e. intersection of constraints and vector averaging which would not predict that adapting to orientation changes motion direction) but allows form information to constrain the overall solution. The model, thus, illustrates a general principle of form-motion interactions, described at a high level. Later studies could apply these principals to models working on natural image sequences.
Figure 9. a-b. A schematic of the model showing how inhibitory (a) or excitatory (b) input from orientation channels to motion channels can cause the observed direction aftereffect. The height of the channel indicates the sensitivity of that channel. The bandwidth parameter of the orientation-selective channels was set to 15° and the motion-sensitive channels were set to 40°. In the examples, a static adapting stimulus is presented with an orientation of 40°, and test at 0°, provides either an inhibitory (a) or excitatory (b) input to the motion channels sensitive to directions of 40° and 220°. The perceived direction of vertical motion is either repelled from (a) or attracted to (b) the adapting orientation. The perceived aftereffect is indicated by the filled in slices of blue (a) or red (b) – note they are on opposite sides of 0°.

The model consists of separate banks of orientation- and motion-selective channels. Orientation is represented in double-angle space, encompassing all 180° of orientation, and motion is represented in single-angle space, encompassing all 360° of motion direction (Clifford et al., 2000). Each channel has a Gaussian sensitivity profile that is centered on its preferred orientation or motion direction. The channel’s orientation- or motion-selectivity is evenly spaced to represent double- or single-angle space (Eqn. 2).
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The perceived orientation or motion direction is encoded in the collective response of the bank of channels. When a stimulus is presented it activates a number of channels within the bank that are preferably sensitive to the stimulus parameters. The perceived motion direction is the vector sum of the response of the motion channels to the test stimulus given their sensitivity profiles to the presented motion direction.

\[ R(x) = \alpha \times \exp \left( -\frac{(x + c)^2}{2\sigma^2} \right) \]

*Equation 2.* A variation of a standard Gaussian equation gives the sensitivity profile \( R \) of each orientation and motion-selective channels in the current model. \( \alpha \) represents the amplitude of the Gaussian profile. \( \sigma \) represents the width of the profile that varies to change the channel’s bandwidth parameter. \( c \) is used to vary the orientation or motion direction that the channel is centered.

The width of the Gaussian sensitivity profiles representing the orientation-selective channels is set at 15° (equivalent to a FWHM of 35°) and the direction-selective channels are set at 40° (equivalent to a FWHM of 94°). Both these values are consistent with considerable neurophysiological and psychophysical evidence of the average tuning for orientation-selective neurons in V1 and motion direction-selective neurons in V5, respectively (Albright, 1984; Britten &Newsome, 1998; Clifford, 2002, 2014; R. L. De Valois, William Yund, et al., 1982; Gibson & Radner, 1937; Rodman & Albright, 1987; Schrater & Simoncelli, 1998; Snowden et al., 1992). This estimate of the V5 bandwidth is inconsistent with motion-selective neurons in V1 that are responsive to 180° of motion direction for extended contours (Movshon et al., 1985).

We chose to base the bandwidth parameters on these locations, as there is very strong evidence that, in humans, adaptation to static gratings cause large changes in V1 (Fang et al., 2005; McDonald, Seymour, Schira, Spehar, & Clifford, 2009; Tootell et al., 1998) and the static orientation cue from the motion streak is detected in this area (Basole,
White, & Fitzpatrick, 2003; Geisler et al., 2001). V5 was chosen because this area has been strongly linked to global motion perception in humans (Beckers & Zeki, 1995; Born & Bradley, 2005; ffytche, Guy, & Zeki, 1996; Morrone, Burr, & Vaina, 1995; Smith, Snowden, & Milne, 1994). Furthermore, V5/MT, unlike V1, contains pattern-selective neurons that are not subject to the aperture problem (Kumano & Uka, 2013; Movshon et al., 1985), with only a small number of the neurons needed to give psychophysical performance on a motion task (Shadlen, Britten, Newsome, & Movshon, 1996).

When an adapting stimulus is presented, the channels that are responsive to that orientation are suppressed (in proportion to their activation to that stimulus, which is given by the Gaussian sensitivity profile for each channel to the orientation of the stimulus). Each orientation-selective channel is linked to the two motion direction-selective channels along the motion axis, due to the change from double- to single-angle space. For example, an orientation-selective channel centered at 40° is linked to two motion-selective channels, one centered at 40° and the other centered at 220°. The orientation-selective channels provide gain (ranging from inhibitory to excitatory) to the motion-selective channels, modifying the sensitivities of the motion-selective channels in proportion to the activity of the corresponding orientation-selective channels during adaptation.

The gain-induced changes in the channel’s sensitivity following adaptation are reflected in contrast sensitivity decreasing following adaptation to the same spatial frequency (Blakemore & Campbell, 1969; Ware & Mitchell, 1974) but increasing when the spatial frequency varies by two octaves (K. K. De Valois, 1977). Changing the gain from inhibitory to excitatory reverses the aftereffects from repulsive to attractive.
(Figure 9a-b), consistent with our empirical findings when the spatial frequency of the adaptor changes by two octaves. The perceived motion direction, given by the population response, is either attracted or repulsed away from the adaptation orientation because during adaptation the sensitivity of the bank of channels has been depressed or elevated around the adapting orientation.

To model the results from the form-only condition, the same bank of orientation-selective channels is used for both adaptation and test. This same model has been used to successfully account for both the repulsive TAE and attractive orientation illusions (Dickinson et al., 2012). To model the results in the motion-adaptor condition, adaptation gain from motion-selective channels feeds into the orientation-selective channels. Because the streak will leave the neural equivalent of an oriented form cue along the axis of motion, additional adaptation of the orientation channels aligned with the motion direction was allowed. This stage could be incorporated into the main motion streak model without affecting the results as the streak is in the direction of the motion stimulus meaning there would be no effect. The model’s only free parameter is the gain between the banks of channels.

The input to the model is the orientation or motion direction of the adapting stimulus that was held throughout the computation as vertical, consistent with the parameters used when gathering the experimental data. The motion direction input was a direction representing the 2D motion vector. This was used because the true motion direction is the dominant signal with the 100% coherent global dot motion stimulus used in the experiment, which allows observers to discriminate motion direction with very high levels of certainty (Edwards & Badcock, 1994; Webb, Ledgeway, & Mcgraw, 2007). The proposed gain relationship between orientation and motion neurons outlined here could allow form information to affect different motion pooling solutions (e.g.
intersection of constraints, vector averaging) in a manner which is currently unpredicted.

We used the model to predict the magnitude of the aftereffect following adaptation to the same orientations and directions used in the experiments measuring the angular dependence of the aftereffects (Figure 10). Extra sum-of-squares F-tests (Motulsky & Christopoulos, 2004) indicated the model’s predictions did not significantly differ from the observed results (all $ps > .05$), suggesting that the model provides a good explanation for the extant results. We can also account for the halving of the SI-DAE when we increased the excitability of V1 using anodal tDCS by reducing gain between orientation- and motion-selective neurons. The model’s predictions are relatively robust to the bandwidth parameters of the motion-selective channels. We examined the effects on the sigma of the resultant D1 function of varying the bandwidth parameter of the motion-selective channels while holding the bandwidth parameter of the orientation-selective channels constant. This showed that after the sigma value of the channels exceeded 40° the estimated angular dependence of the aftereffect remains relatively constant (Figure 11).
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**Figure 11.** The effects of varying the bandwidth parameter of the motion-selective channels on the width of the angular dependence estimated by fitting the results with the D1. Here we varied the bandwidth parameter of the motion-sensitive channels while holding the bandwidth parameter orientation-selective channels constant at 15°. The error bars represent the 95% confidence intervals associated with the goodness of fit to the stimulated data.
3.6 Conclusions

Our results demonstrate that motion streaks, which arise from the extended integration time of neurons in V1 yielding the neural equivalent of a form cue along the axis of motion, contribute to the perceived direction of motion by a different neural mechanism than is currently thought. The dominant model argues that orientation-selective neurons in V1 detect the streak and that this information is combined in the same stage with motion-sensitive neurons in the same area (Geisler, 1999; Geisler et al., 2001). Our results, instead, suggest that streak-inducing motion stimuli are detected by narrowly-tuned orientation-selective neurons at an early stage, which feed gain into direction-selective neurons at a later stage of motion processing, most likely V5, the stage of global motion integration. This conclusion follows because the aftereffect was reduced when the excitability of V1 was increased using tDCS, suggesting the involvement of V1, and because of the broad tuning and spatial-frequency dependency of motion aftereffects, which suggest the involvement of V5.

We created a computational model with narrowly-tuned orientation-selective neurons (purportedly in V1) feeding gain into broadly-tuned motion-selective neurons (proposed to be in V5) that accurately describes these results. This model is consistent with previous research showing that motion streaks activate orientation-selective neurons in V1 (Apthorp et al., 2013; Basole et al., 2003; Geisler et al., 2001), but adds a unique interaction with motion processing at a higher stage. Unlike most existing theories, we suggest that the streak information gathered at an earlier stage first influences motion direction processing at a later stage of the processing hierarchy. We believe that V5/MT is the later area of processing for a number of reasons. Firstly, neurons in this area are broadly tuned, consistent with the broad angular dependence of
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determine the motion streak aftereffect (Albright, 1984; Snowden et al., 1992). Secondly, IOC-like information appears to be first integrated in this area from direction-selective input from V1 that are subject to the aperture problem (Heeger et al., 1996; Kumano & Uka, 2013; Movshon & Newsome, 1996). It, therefore, seems possible that orientation information, also gathered in V1, inputs the motion direction computation at this later processing stage in the manner described.

While clearly not a definitive description of the visual system, we believe that our model provides a significant advance in understanding how form information can constrain motion processing. Indeed, the model can account for a variety of phenomena in the empirical literature. The model is consistent with our recent demonstration that form information enters the motion system by, at least, the stage of global motion pooling (Tang, Dickinson, Visser, Edwards, & Badcock, 2013). The model also explains why the presence of a motion streak enhances contrast sensitivity for both single moving dots (Geisler, 1999) and global motion (Edwards & Crane, 2007). The model predicts that the orientation cues from motion streaks could enhance the motion signal through gain adjustments when they are coincident with the motion direction leading to increased motion direction sensitivity. Additionally, the same mechanism described in the model can also explain why providing orientation information at the edge of apertures or adding oriented static lines to the background of a display changes the perceived direction of motion (Badcock et al., 2003; Edwards, Cassanello, Badcock, & Nishida, 2013; Khuu, 2012; Kooi, 1993).

The model also provides a description of why presenting Glass patterns without any consistent motion signal, but with a consistent global pattern, results in the perception of motion in the global pattern direction (Badcock & Dickinson, 2009; Ross, 2004; Ross et al., 2000). Consistent with the model, these patterns activate motion
The broad orientation dependence of the motion streak aftereffect reveals interactions between form and motion neurons sensitive areas in human (V5) and macaque (STS) (Krekelberg, Dannenberg, Hoffmann, Bremmer, & Ross, 2003; Krekelberg, Vatakis, & Kourtzi, 2005). The perception of motion in the pattern direction would occur because the form information enhances a motion representation in the consistent direction. The undirected motion energy, therefore, causes the greatest activation coincident with the pattern orientation.

3.7 Summary

Our study shows that form information influences motion processing in a different manner than previously thought. Our results reveal that the orientation cues from motion streaks, which are detected in V1, influence motion direction processing at a later stage, most likely V5. We provide a new model of motion direction that gives a systematic explanation of how form information enters the motion system, which is unaccounted for by existing models of visual processing. This is important for understanding how the visual system recovers object motion as it shows that form information provides a strong constraint on motion processing.

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3.9 References


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4 Visual orientation information has direct gain inputs at the stage of global motion integration

Matthew F. Tang, J. Edwin Dickinson & David R. Badcock

School of Psychology, The University of Western Australia, Crawley, Western Australia, 6009, Australia.

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Chapter 4: Visual orientation information has direct gain inputs at the stage of global motion integration

4.1 Foreword

The previous chapter examined an influential model of a form-motion interaction. The original model (Geisler, 1999) argued that form information from motion streaks is multiplicatively combined with motion information in V1, resulting in motion signals inheriting the orientation fidelity of the form information. There have been a number of studies providing evidence that motion signals do indeed leave the neural equivalent of form signals along the motion path in V1 (Apthorp & Alais, 2009; Apthorp, Cass, & Alais, 2010; Apthorp, Cass, & Alais, 2011; Apthorp et al., 2013; Apthorp, Wenderoth, & Alais, 2009; Geisler et al., 2001). However, Chapter 3 was the first comprehensive test of how the orientation information from the streak is combined with motion direction information. The results suggested that form information from motion streaks enters the motion system by, at least, the stage of global motion integration, most likely V5 (Tang, Dickinson, Visser and Badcock, 2015).

A new model of motion streaks was provided to account for these results. Narrowly-tuned orientation-selective neurons directly influences broadly-tuned motion-selective neurons at a later stage of processing. The model states that each orientation-selective neuron directly modifies the gain of linked motion-selective neurons. For example, an orientation-selective neurons maximally selective at 40° is linked to maximally motion-selective neurons at 40° and 220°. A unique prediction of this model is that orientation-selective neurons are directly linked to motion selective neurons at the stage of global motion integration. This means that any orientation signal will alter the gain of motion-selective neurons at the stage of global motion integration. Chapter 4 sought to determine whether orientation signals directly influence motion-selective
neurons at the stage of global motion integration. The chapter, therefore, provides a strong test of our proposed model.

References


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4.2 Summary

One of the fundamental tasks of the visual system is to track moving objects as they move through the environment. Models of visual processing have generally argued that the object’s form and motion components are separately processed [1, 2]. There is now, however, growing evidence that an object’s form influences its perceived direction [3, 4], suggesting that these processes influence each other at relatively early stages. The locus of this interaction, however, currently remains uncertain. Here we present a strong demonstration that orientation information directly influences the stage of global motion pooling, most likely in V5/MT. We show that adapting to a static grating alters the perceived direction of a subsequently-presented motion stimulus. The motion stimulus comprises many spatially-separate patches of two-component textures (plaids), the orientations of the component pairs are randomized, while the drift rates are made to be consistent with a global motion solution [5]. The orientation randomization of the component pairs means the aftereffect cannot be due to adaptation affecting each individual grating and is, instead, due to orientation adaptation affecting the stage of global motion integration where velocity signals are combined [6]. We then show this gain relationship can be either inhibitory or excitatory depending on the spatial frequency of the adaptor, with perceived motion direction changing from being repelled to attracted by the adapting orientation. We conclude with a strong test of our thesis showing global motion sensitivity can be either improved or degraded depending on the spatial frequency of the adaptor.

4.3 Results

In this study, the suggestion that orientation information directly influences global motion-selective neurons is evaluated using visual aftereffects. A prediction from
a recently proposed form-motion model [7], which consists of narrowly-tuned orientation-selective neurons directly modulate the gain of broadly-tuned global motion-selective neurons, is that adapting to a static pattern orientation will change the perceived direction of motion which is only signaled by neurons selective for global motion [7]. The magnitude of perceived direction repulsion was measured for a motion stimulus, following adaptation to a static oriented Gabor patch (a sinusoidal grating modulated by a 2D Gaussian weighting function, see Figure 1D). The motion stimulus consisted of 208 spatially-separated small plaid elements (two summed sinusoidal gratings with orthogonal orientations modulated by a 2D Gaussian weighting function) contained in the same area as the adapting stimulus, with the orientations of the plaid pairs randomized on each trial (Figure 1A). The perception of global motion is created by setting the drift rates of the plaid carriers to be consistent with a globally-defined motion direction [8, 9]. The local aftereffects cannot cause the perceived change in motion direction because the orientations of the local elements are randomized across the array, meaning that the average local aftereffects would be nulled (Figure 1E). Any perceived change in direction of the test stimulus would, therefore, be due to the adaptor affecting the stage of global motion integration where these signals are combined [5].
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Figure 1. A. A static example of the motion-test stimulus. B. A subset of 4 plaid from A (indicated by the blue square) and their velocity-space representation. The dotted black arrows indicate the directions of the components with the colored arrow showing the global motion solution, given through the intersection of constraints. C. The colored circles around each Gabor match the colored lines of the vectors in C. The direction of the vector represents the local direction (perpendicular to the plaid’s orientation) and the length represents the velocity. The dotted lines that are perpendicular to each vector represent the constraint lines, indicating a range of directions and speeds consistent with the same orthogonal velocity estimate. The intersection of these four lines represents the global motion solution (in this case vertical). D. A schematic representation of a trial. E. A demonstration why local aftereffects fail to account for the perceived change in direction with the global plaid stimulus. Each blue dot represents the actual plaid orientation (averaged between the two component orientations) in the motion array. The perceived orientation of the plaid is predicted by convolving the actual orientation with a standard local aftereffect function [10] in the right panel. The perceived orientations average to 0° as the local aftereffects are symmetrical either side of the adapted orientation.
Adapting to static orientation did indeed change the perceived direction of motion of the global plaid stimulus (Figure 2, Movie 1). The magnitude of perceived direction repulsion depended on the orientation/direction difference between the adapting Gabor and global motion direction, with the largest aftereffect occurring when the adaptor and test were separated by ~35°. This angular dependence is similar to the standard motion direction aftereffect [11, 12] and double that usually found for orientation aftereffects [13, 14] and thus further provides support for adaptation affecting the stage of global motion integration. This is because direction aftereffects, thought to be associated with changes at this stage [15] cause a broad tuning of aftereffects whereas orientation aftereffects are usually thought to be associated with changes at V1 [16, 17], result in a significantly narrower range of orientations causing aftereffects. Our model [Figure 4, 7] where narrowly-tuned orientation-selective neurons modulate the gain of broadly-tuned motion selective neurons, accurately predicts the measured angular dependence of this aftereffect (Figure 2) suggesting that this mechanism, outlined in the model, is causing the change in perceived direction.
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Figure 2. The angular dependence of the after-effect (points) and the predicted direction from our model (solid line) (n = 3). A positive value of the adaptor orientation indicates the adapting grating is rotated anti-clockwise from vertical, while positive indicates clockwise rotation. A positive aftereffect indicates the observer perceived vertical test stimuli as clockwise of vertical, while negative indicates vertical was perceived as anti-clockwise from vertical. Response bias has been removed from results (see methods). Error bars represent ± 1 standard error.

We next sought to build on this demonstration that orientation can directly influence the stage of global motion integration by examining the spatial-frequency dependency of the after-effect. Neurons in V1 only respond to a limited range of spatial frequencies [18]. Psychophysical results reflect this neurophysiology with form aftereffects (i.e. the tilt aftereffect and illusion), associated with changes in V1, only occur when the adapting and test stimuli have similar spatial frequencies [14, 19]. Neurons at the stage of global pooling, however, integrate signals across a large range of spatial frequencies [20, 21] as indicated by psychophysical results showing that global motion processing also pools across a wide range of spatial frequencies [22, 23].

The spatial frequency of the adapting grating was varied to test our belief that orientation is affecting the stage of global motion integration. The orientation of the adaptor was held at 30°, as this produced the largest aftereffects. Varying the spatial
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frequency of the adaptor caused the aftereffect to change from repulsive to attractive when there was more than a two-octave difference between the adaptor and test stimulus (Figure 3A, Movie 2). This finding is consistent with our recent results where the alteration of perceived direction of streak-causing motion changes from attraction to repulsion depending on the spatial frequency of the adaptor [7]. Repulsive aftereffects are thought to result from orientation-selective reductions in contrast sensitivity following adaptation, reflected in the decreased firing rates of adapted neurons [24]. Contrast sensitivity, however, increases when the adaptor and test are separated by two octaves [25] producing an increase in firing rate that causes the perceived motion direction to be attracted towards the adapted orientation (see modeling section).

![Figure 3. A](image1.png)  
Figure 3. A, The magnitude of the aftereffect (perceived difference from vertical) when the spatial frequency of the adaptor was varied. Positive values indicate repulsive aftereffect while negative numbers indicate attractive aftereffects. The orientation of the adaptor was kept at 30° from vertical in all conditions. The arrow indicates the spatial frequency of the test stimulus (n = 3). B, Coherence thresholds for vertical motion (3 c/°) presented after adapting to a vertically-oriented static adaptor (n = 4). Error bars represent ±1 within-subject standard error.
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We next built upon the two previous findings suggesting that orientation is directly impacting the stage of global motion integration in a spatial frequency-dependent manner. This suggestion was assessed by determining whether global motion coherence thresholds, which are strongly associated with sensitivity of neurons in MT/V5 [26, 27], are affected by adapting to static orientation. We compared global motion coherence thresholds for a vertically-moving global plaid stimulus, after adapting to vertically-oriented static gratings of with spatial frequency either the same (previously shown to cause direction repulsion) as, or two octaves different (shown to cause direction attraction), to the motion-test stimulus (Figure 3B). Our model predicts that direction repulsion is caused by decreased sensitivity in global motion neurons while attraction is caused by increased sensitivity. In support of our hypothesis, global motion thresholds were affected by adaptation to a static grating in a spatial-frequency dependent manner, consistent with that required to predict the change in aftereffect from repulsive to attractive as a function of the spatial frequency of the adaptor, \( t(2) = 9.38, p = .01, R^2 = .98 \).

4.4 Discussion

This study provides the first evidence that static form information directly influences motion-selective neurons at the stage of global motion integration. Adapting to an oriented static grating changes the perceived direction of the global plaid stimulus in a manner that cannot be due to local aftereffects. Spatial orientation adaptation either repelled or attracted perceived motion direction depending on the spatial frequency relationship between the adapting and test stimulus. We next provided further evidence that orientation alters the gain of global-motion selective neurons as motion coherence thresholds were also systemically altered by this procedure. This pattern of results can
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be described if narrowly-tuned orientation-selective neurons directly influence the gain of broadly-tuned motion-selective neurons at the stage of global motion integration. The measured orientation-dependence of the repulsive aftereffect was predicted when we implemented a simple version of this model where orientation-selective neurons in V1 systemically modulate the gain of motion-selective neurons in V5/MT based on the average tuning bandwidths reported for these areas [28, 29].

Global motion integration is strongly associated with MT in primates [6, 28] and its functional equivalent in V5 in humans [27, 30]. MT/V5 receives most of its inputs from V1 [6] suggesting that it is likely that the orientation information enters the motion system through this direct connection. There are also extensive connections between V4, which is strongly associated with shape processing, and V5 [31-33] that could also allow for gain modulation of the motion representations. While there is recent evidence that area V3a is selective for global motion [30, 34], we believe it is more likely that V5 is the source of the reported results as this area shows far greater response to the global plaid stimulus than V3a [27]. Furthermore, human behavioral performance is strongly correlated to single cell response in V5 when using global dot motion stimuli [35]. However, further work is needed to determine the exact neural locus of this interaction.

Our results provide a mechanism that explains a number of psychophysical and neurophysiological effects. Presenting a series of patterns with a randomized local structure, but consistent global pattern results in the perception of motion in the global pattern direction [36]. This unique motion stimulus causes strong activation area STS in macaque [37] and area V5 in humans [38]. Motion is perceived in the pattern direction because the consistent orientation information enhances the global representation of the motion axis thus the random undirected motion causes greatest response in this
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direction. The model also explains why these stimuli are perceived as bi-stable, rocking back-and-forth along the pattern orientation, as the pattern enhances an axis, but not a single direction, of motion (e.g. 40° and 220°). The model also reconciles two seemingly contradictory findings that form cues arising from motion streaks facilitate detection of motion [39, 40] but do not improve the fidelity of direction discrimination [41]. This is because orientation enhances motion along the same axis without affecting the bandwidth, the parameter that underlies discrimination fidelity, of the neurons sensitive to global motion. Consistent with this notion, the orientation cues intrinsic to biological motion, where a small number of dots give the vivid impression of a living creature, could explain the increased sensitivity to biological motion compared to motion signals without these form cues [42]. Furthermore, the model predicts the perceived direction of motion in the classic barber pole illusion [43] where perceived direction follows the orientation of the aperture shape or of background lines (demonstrated in Chapter 5) [44]. A large amount of existing data can, therefore, be explained by accepting that orientation constrains motion processing at the stage of global motion integration.

Overall, the results suggest that it is important to consider an object’s orientation content to determine how the visual system estimates its direction. This is contrary to most theories of visual perception, which are predicated on the assumption that form and motion are processed in relatively separate neural pathways. These results build upon recent evidence that form can enter the motion system by the stage of global motion pooling [7, 45]. The model outlined provides a mechanism to explain how orientation constrains motion processing and, importantly, in conjunction with the data,
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shows that form information must be considered when attempting to understand motion processing.

4.5 Experimental Procedures

4.5.1 Observers

Four observers (3 males, 1 female) between the ages of 23 and 50 yr (median = 26.5 yr) participated across the experiments with three included in each experiment. All had normal or correct-to-normal acuity as assessed by a LogMAR chart and provided written informed consent. The procedure was approved by the UWA Human Research Ethics Committee and was in accordance with the Declaration of Helsinki.

4.5.2 Apparatus

The stimuli were generated in MATLAB 7.14 on a MacBook Pro (i7, 2.53 GHz) with a NVIDIA GT650M graphics card. The stimuli were presented using PsychToolbox [46, 47] on a Sony Trinitron G520 monitor, with a 120 Hz refresh rate and 1024 × 786 pixels resolution. Observers viewed the monitor from 70 cm, maintained using a chin rest, at which distance the screen subtended 31° × 23° (each pixel subtended 1.8’ × 1.8’). The luminance was gamma-corrected using a Cambridge Research System ColorCAL II and custom-written software. The background of the monitor was set at a mid-gray with a luminance of 80 cd/m², and the maximum white luminance was set at 160 cd/m².

4.5.3 Stimulus and Procedure

Each trial began with a centrally-presented fixation point. An adapting Gabor was then presented for 1.5 s followed by a 160 ms inter-stimulus interval before the 160 ms motion stimulus was presented. The observers indicated whether the direction of the test motion was to the left or right of vertical. The standard deviation of the envelope of
the adapting Gabor was 2.66° and it had a carrier spatial frequency of 3 c/° unless otherwise noted. The test motion stimulus was adapted from the global Gabor array [5, 48, 49]. 208 plaid elements were presented in an ordered grid contained within a 10° circular aperture (Figure 1A). The orientations of the two plaid components in each element were separated by 90°, oriented symmetrically either side of a common patch orientation, which were randomly assigned at the beginning of each trial. Plaids were chosen rather than Gabors because these produce a stronger sense of directional motion. A small number of observers were, however, also tested with Gabors as the test stimulus and the same broad orientation dependency was found. To give the impression of global motion, the drift rates for each component in the elements was set to be consistent with a intersection-of-constraints defined global motion solution representing rigid translation, given by the cosine function of the difference between the component orientation and desired global vector (Figure 1C). The motion sequence consisted of 8 frames, each presented for 3 monitor refreshes (an effective frame rate of 40 Hz), meaning that the test stimulus was presented for 160 ms.

The orientation of the adaptor was varied between -90° and 80° from vertical in 10 steps to measure the angular dependence of the aftereffect in the initial experiment. The intersection-of-constraints defined global motion direction [9] of the test stimulus was varied using the method of constant stimuli, with the step size adjusted to measure each observer’s entire psychometric function. In each block of 140 trials, there were 20 trials for each of the 7 evenly-spaced motion directions defined by the method of constant stimuli. The observer’s completed 2 blocks of trials for each condition. To estimate the magnitude of the aftereffect, the probability of the observer responding that the stimulus was moving to the right of vertical was calculated for each veridical test
motion direction in each adaptor condition. Cumulative Gaussian functions were fitted to these responses in GraphPad Prism (6.0c for Mac, GraphPad Software, CA, USA) with the mean indicating the point of subjective equality, reflecting the veridical motion direction required to appear to move vertically after adaptation.

Except where noted, the same procedure and stimulus was used to measure motion coherence. The drift rates of each Gabor were made to be consistent (or not) with the global motion solution by varying the motion coherence of the test stimulus. X% of elements with the global intersection-of-constraints solution defining the motion coherence level with the remainder of the plaid's (100-X%) assigned noise directions. A two-interval forced-choice, three-down, one-up adaptive staircase procedure was used to estimate the 79.4% global motion threshold for each condition [50]. One interval contained a motion test with signal and the other had 0% coherence with the observers required to indicate which interval contained coherent motion. All staircases began with 100% coherence (208 elements) and were reduced by 8 signal plaid elements after each correct response until the first mistake was made. The step size was then halved after each of the next two staircase reversals, and then maintained at 1 for the final six reversals. The staircase terminated after 8 reversals and the threshold was taken as the mean number of signal elements during the final 4 reversals. Auditory feedback was given following each response before the next trial was initiated. The observers completed 5 staircases for adaptor condition.

4.5.4 Modeling

The model consists of two separate banks of 18 neurons each; the first representing narrowly-tuned orientation-selective neurons and the second representing broadly-tuned motion-direction-selective neurons (Figure 4). We have extensively documented the model earlier with all the same parameters used [7].
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Figure 4. A schematic diagram of our model how static orientation constrains motion processing. A. The bank of orientation-selective neurons. The lines indicate each neuron’s sensitivity profile to different orientations. Each red dot represents the corresponding neuron’s response to a static adaptor with a 90° orientation. B. The bank of motion-selective neurons with each neuron linked to a corresponding orientation-selective neuron (links shown by matching x axis values). The sensitivity profiles have been depressed in proportion to the corresponding orientation-selective neuron’s response (in this case at 90° and 270°) to the adapting stimuli and the gain factor (in this case 2). The blue dots show each neuron’s response to a 100° motion stimulus prior to adaption and the yellow dots show the adapted response. The signaled motion direction is given by the vector sum of the responses.

Each neuron is represented by Gaussian sensitivity profiles that are evenly spaced over 180° for orientation and 360° for motion (Equation 1).

$$R(x) = \alpha \times \exp \left(-\frac{(x + c)^2}{2\sigma^2}\right)$$

(2)

Equation 2. A variation of a standard Gaussian equation gives the sensitivity profile (R) of each orientation and motion-selective channels in the current model. \(\alpha\) represents the amplitude of the Gaussian profile. \(\sigma\) represents the width of the profile that varies to change the channel’s bandwidth. \(c\) is used to vary the orientation or motion direction that the channel is centered.

The bandwidths of the sensitivity profile were set to be consistent with commonly reported mean full-width at half-height bandwidth for orientation-selective neurons in V1 [29, 51] and motion-selective neurons in V5 [28, 52, 53] of 35° and 94° respectively. We based the bandwidths of neurons on these cortical areas because V1 is
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strongly associated with orientation-selective responses [54] and changes with adaptation to orientation [24], and V5/MT is strongly associated with global motion integration [6, 21, 26]. When the adapting stimulus is presented, it reduces the sensitivity of the orientation-selective neurons to that stimulus, in proportion to the unadapted sensitivity profile (i.e. the adjustment is proportional to the strength of response). The orientation-selective neurons are linked to motion-selective neurons along the same axis, thus an orientation neuron at 40° is linked to motion neurons at 40° and 220°. The orientation-selective neurons provide either inhibitory or excitatory gain to the linked motion-selective neurons. The sensitivity of the motion-selective neurons is altered by the response of the linked orientation-selective neurons to the adapted orientation and the gain parameter, the model’s only free parameter. The signaled motion direction is given by vector sum of the population response of the motion-selective neuron to the presented motion direction. Orientation can either attract or repel the perceived motion direction depending on whether the gain is inhibitory or excitatory. The amount of gain mainly determines the magnitude of aftereffect with relatively little effect on the predicted angular dependence of the aftereffect, consistent with psychophysical results [13].
4.6 References


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5 The shape of a moving object changes its perceived motion direction

Matthew F. Tang, J. Edwin Dickinson & David R. Badcock

School of Psychology, The University of Western Australia,
Crawley, WA, Australia

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Chapter 5: The shape of a moving object changes its perceived motion direction

5.1 Foreword

The previous chapter provided a strong test of our proposed form-motion model. The model uniquely shows that narrowly-tuned orientation-selective neurons, most likely at V1, modulate the gain of broadly-tuned motion selective neurons at the stage of global motion integration. The model was developed to account the unexpectedly broad orientation dependence of the motion streak aftereffect (Chapter 3, Tang, Dickinson, Visser and Badcock, 2015). The original model of motion streaks (Geisler, 1999) argued that the orientation cue from the motion streak is multiplicatively combined with motion information in V1. This multiplicative combination means that motion information is processed like form, which would have predicted narrower tuning. The explicit assumption from the original model is that the form information is necessarily produced by motion streaks. Our proposed model instead argues orientation directly modulates the gain of motion-sensitive neurons at a later stage. The study presented evidence that orientation has a direct influence on motion at the stage of global motion integration (Tang et al., 2015). The next chapter builds on this finding to show that an object’s shape will change its perceived motion direction.

The two previous chapters (Chapter 3 and 4, Tang et al., 2015) used adaptation to investigate the role of form information in motion processing. But, real-world objects have both form and can generate motion signals. This form and motion simultaneously arrives at the visual system, whereas the previous chapters presented separate orientation then motion. This chapter aims to generalize the newly-proposed form-motion model, which was developed to account for adaptation results, to simultaneously-presented form and motion signals. The two previous chapters could then be considered the form-motion equivalent of the tilt aftereffect, where adapting to an oriented feature repels the perceived orientation of subsequently presented features.
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The current chapter could, however, be considered the form-motion equivalent of the tilt and twisted cord illusions, where the orientation of a feature is either attracted or repelled of simultaneously-presented features. It will be shown that the orientation information of moving objects changes the perceived direction in a manner predicted by the proposed model. The importance of this chapter is to show that the shape of a moving object will determine how observers perceive its motion direction.

References


Chapter 5: The shape of a moving object changes its perceived motion direction

5.2 Abstract

Visual form and motion information are generally considered to be processed in separate, functionally-distinct neural pathways. While there is a large amount of neurophysiological and psychophysical evidence showing these processes are often largely independent, more recently studies have suggested that interactions actually occur at early stages of processing. Here we present a unique model where orientation information, extracted by narrowly-tuned neurons in V1, directly modulates the gain of broadly-tuned motion-selective neurons at the stage of global motion integration. A new illusion is presented where the perceived direction of a moving stimulus can be either attracted or repelled from its trajectory depending on its orientation and spatial frequency. Allowing the form of moving objects to directly modulate the activity of the motion-selective neurons allows the model to explain a number of psychophysical illusions where motion direction and perceived position is influenced by the form information. The results strongly suggest that, contrary to one prediction from many of the existing models of visual processing, the shape of a moving object dramatically influences its perceived motion direction.
5.3 Introduction

One of the fundamental tasks of the visual system is to track objects as they move through the world. Most models of visual processing are predicated on the belief that form and motion information are functionally distinct and do not influence each other. These models were developed in light of neurophysiological evidence that form and motion information are processed in separate neural pathways and psychophysical evidence showing that these types of information can be dissociated (Braddick, O'Brien, Wattam-Bell, Atkinson, & Turner, 2000; Livingstone & Hubel, 1987; Mishkin, Ungerleider, & Macko, 1983). The common view is that motion direction is given by a decomposed representation of a moving object in frequency space (Adelson & Bergen, 1985; Heeger, 1987; Heeger & Simoncelli, 1992; Heeger, Simoncelli, & Movshon, 1996; Watson & Ahumada, 1985). Motion direction is signaled by the successive activation of two spatiotemporally direction-selective neurons oriented in the motion direction. This conceptualization of motion direction means the object’s shape does not separately influence the signaled direction.

There is, however, a growing body of evidence which shows that the existing assumptions are incorrect and instead shows form and motion interacting at early stages of the visual processing hierarchy (Nishida, 2011). One such interaction is through motion streaks, where the extended integration time of neurons in V1 leads fast moving objects to leave the neural equivalent of a streak along the axis of motion (Apthorp & Alais, 2009; Badcock & Dickinson, 2009; Burr, 1980; Burr & Ross, 2002; Geisler, 1999; Geisler, Albrecht, Crane, & Stern, 2001; Ross, Badcock, & Hayes, 2000). These form cues increase sensitivity to enhance recovery of motion signals and can also influence perceive direction (Apthorp et al., 2013; Edwards & Crane, 2007; Geisler, 1999). We have recently shown that altering the orientation information derived from
motion streaks, by adaptation, changes the perceived direction of motion (Tang, Dickinson, Visser, & Badcock, 2015). The broad range of orientations that caused aftereffects suggested that the form information first influences motion processing at the stage of global motion integration, most likely V5.

A model was developed which successfully accounted for the broad effect of orientation adaptation on motion direction. This model provides a simple constraint on motion direction processing. The important and novel contribution of the model is that narrowly-tuned orientation-selective neurons in early visual cortex (likely V1) directly modulate the gain of broadly-tuned motion-selective neurons at the stage of global motion pooling (most likely V5/MT or MST) along the matching orientation axis (Figure 1). For example, an orientation-selective neuron centered at 40° is linked to two neurons at 40° and 220° corresponding to the motion axis. This orientation-specific constraint on motion direction can either be inhibitory or excitatory, thus suppressing or enhancing the motion representation. Both inhibitory and excitatory gain was incorporated to account for a surprising finding showing that adaptation to orientation could either attract or repel perceived motion direction depending on the relative spatial frequency of the adapting and test stimuli (Tang et al., 2015). Overall, the model argues that form information enters the motion system at the stage of global motion integration. Furthermore, the form information will inherently constrain motion processing in a previously-undescribed manner.
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Figure 1. A schematic representation showing how the model operates. The number of neurons in the banks of form and motion channels has been reduced from 32 to 18 for clarity. Furthermore, the model’s predictions are largely independent of the number of channels. There are two separate banks of neurons, either representing orientation (A) or motion direction (C-D). The orientation-selective neurons are narrowly tuned (20°) whereas the motion-selective neurons are broadly tuned (40°). A. The unbiased sensitivity profiles for orientation-selective neurons. The red dots show the response for each neuron when an orientation of 50° is presented. B. The corresponding gain changes for the 50° orientation, with the yellow dots indicate inhibitory gain whereas the blue dots show excitatory gain. C. The sensitivity profiles for the motion-selective neurons are modulated by the inhibitory response in B. D. The sensitivity profiles for the motion-selective neurons are modulated by the excitatory response in B. The colored dots in C-D show the adapted population response, which is either repelled away from (C) or attracted to (D) the presented orientation.

The finding that form-motion aftereffects can be attractive was surprising as aftereffects are generally repulsive. For example, the tilt aftereffect generally shows that the orientation of a line will appear to be tilted away from an adapted orientation, that is it is repelled by the adaptor (Gibson & Radner, 1937). This is consistent with the majority of other aftereffects where adaption increases the perceived difference between the adapted and test features (Burr & Ross, 2008; McCollough, 1965; Rhodes, Jeffery, Watson, Clifford, & Nakayama, 2003; Webster, 2011) (but see (Fischer & Whitney,
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But, the perceived feature can be attracted towards the adapted feature in some limited circumstances (O'Toole & Wenderoth, 1977; Wenderoth & Johnstone, 1988). The repulsive tilt aftereffect is associated with the bias in population response for orientation-selective neurons for nearby, but not distant, orientations (Dragoi, Sharma, & Sur, 2000). The reduction in neuronal sensitivity following adaptation causes a corresponding reduction in contrast sensitivity for both nearby orientations and spatial frequencies (Blakemore & Campbell, 1969; Ware & Mitchell, 1974). Contrast sensitivity, however, has been shown to increase when spatial frequency of the adaptor and test stimulus are separated by ~2 octaves (K. K. De Valois, 1977). This increase in contrast sensitivity when the adaptor and test stimuli have broadly different spatial frequencies can explain attractive aftereffects observed in the twisted cord and motions streak illusions (Dickinson, Harman, Tan, Almeida, & Badcock, 2012; Tang et al., 2015).

The proposed form-motion model was designed to account for motion direction repulsion following adaptation to static form. This aftereffect is a form-motion equivalent of the tilt aftereffect, where perceived orientation is repelled following adaptation to static form (Gibson & Radner, 1937). The tilt illusion is the spatial contextual analogue to the temporal tilt aftereffect, with the perceived orientation of a line being directly influenced by the orientation of the surrounding scene (Figure 2; Clifford, 2014; O'Toole & Wenderoth, 1977). Furthermore, the related twisted cord illusion changes from repulsive to attractive depending on the spatial frequency of the carrier and the size of the envelope (Dickinson et al., 2012; Skillen, Whitaker, Popple, & McGraw, 2002). Like the TAE, there are corresponding neural changes with the tilt and twisted cord illusions (Albright & Stoner, 2002; Gilbert & Wiesel, 1990; Sengpiel, Sen, & Blakemore, 1997). Additionally, there are arguable form-motion equivalents of
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The tilt illusion with growing evidence showing that the shape of an object also appears to change its perceived drift direction (Nishida, 2011; Weiss, Simoncelli, & Adelson, 2002). The influence of orientation on perceived motion direction can be thought of as a form-motion analogy of the tilt illusion.

![Figure 2](image1.png)

**Figure 2.** An example of the tilt (A) and the twisted cord (B-C) illusions. A. The orientation dependence of the tilt illusion. In all four cases, the central grating has the same vertical orientation, but the perceived orientation is repulsed away from the surrounding orientations. B-C. The lines are parallel in both cases but appear angled because the illusion shows the carrier orientation either attracting (B) or repelling (C) the perceived position of the envelope.

The current study examines how the shape of a moving object affects its perceived motion direction and determines whether this interaction follows the predictions of our proposed model. We begin by presenting a new illusion showing that form repels perceived motion direction, the magnitude of which is determined by the orientation-direction relationship and is predicted by the new model. Furthermore, the aftereffect can change from repulsion to attracted depending on the spatial frequency. These initial results allow us to show that four previously-published illusions (Anstis, 2012; Badcock, McKendrick, & Ma-Wyatt, 2003; Farrell-Whelan & Brooks, 2013;
Magnussen, Orbach, & Loffler, 2014; Ross, 2004), where orientation attracts or repels the perceived motion direction, are shown to also be accounted for by the model. These results strongly suggest that orientation information directly influences the gain of motion-selective neurons in the specified manner. The results show that form places strong constraints on motion processing in a manner that is unaccounted for by existing motion models.

5.4 Methods

5.4.1 Form-motion model

The model consists of two separate banks of neurons representing cortical neurons selective for orientation and motion direction (Figure 1). The neurons are represented by Gaussian sensitivity profiles (Equation 1), evenly spaced in orientation and direction.

\[ R(x) = \alpha \times \exp\left(\frac{(x + \theta)^2}{2\pi\sigma^2}\right) \]  

(1)

Where the free parameters are: \( \alpha \) the amplitude, \( \sigma \) the width of the channels, and \( \theta \) the orientation or motion direction that the channel is centered on. Orientation is represented in double-angle space around 180° while motion is represented in single-angle space over 360° (Clifford, 2002). The population response is obtained from the sensitivity profiles of the neurons for a given orientation or direction. The signaled motion direction is given by the collective population response represented in the bank of neurons. The perceived motion direction is given by the argument of the vector sum of the response of the motion channels to the test stimulus given their sensitivity profiles to the presented motion direction. Note that this is deriving a motion direction estimate from the collective population channel response, not a combination of derived component directions. Furthermore, because the channels are evenly distributed across
motion directions, vector averaging, sum and intersections of constraints would produce the same direction output for a motion input. A number of neurons activate when a stimulus is presented (either orientation or motion direction), with each neuron’s activation given by the relationship between its sensitivity profile and the stimulus’ orientation or direction. The orientation-selective neurons maximally regulate the gain of the motion-selective neurons along the same axis of motion. For example, when an orientation of 40° is presented, it maps onto motion-selective neurons tuned to 40° and 220° with the change from single to double-angled space (Clifford, 2002).

The full-width at half-height measurements of the channels were set to be consistent with the averaged bandwidths for orientation-selective neurons in V1 (40°) and motion-selective neurons in V5 (95°) estimated from both neurophysiology and psychophysics (Albright & Stoner, 2002; Blakemore & Campbell, 1969; Britten & Newsome, 1998; R. L. De Valois, William Yund, & Hepler, 1982; Snowden, Treue, & Andersen, 1992). The orientation-selective channels modulate the gain of the motion-selective channels through this mechanism. The amount of modulation between the two banks of channels is controlled by the gain. Changing the gain from inhibitory to excitatory changes the orientation from repulsing to attracting the perceived direction of motion. The change between inhibitory and excitatory could occur through changes to the contrast sensitivity function, analogous to the effects following adaptation to different orientations (Blakemore & Campbell, 1969; K. K. De Valois, 1977)

The model takes the orientation and resolved motion direction as inputs, so we have assumed that the aperture problem has been solved prior to these computations with each initial motion signal giving a 2D estimate of signal direction (Amano, Edwards, Badcock, & Nishida, 2009). This characteristic means that constraining motion direction processing with orientation could be incorporated into existing models.
of motion integration (i.e. intersection of constraints, (harmonic (Johnston and Scarfe, 2013) or regular) vector averaging. Here we wished to provide clear evidence that a simple model, with only the aforementioned attributes, can predict a number of seemingly unrelated illusions.

5.4.2 Psychophysical testing

5.4.2.1 Participants

Three observers (all males) between the ages of 23 and 50 yr (median = 28 yr) participated, two in the angular dependence experiments and three in the spatial frequency experiment. All had normal or correct-to-normal acuity as assessed by a LogMAR chart and provided written informed consent. The procedure was approved by the UWA Human Research Ethics Committee and was in accordance with the Declaration of Helsinki.

5.4.2.2 Apparatus

The stimuli were generated in MATLAB 8.1 on a PC running OS X 10.9 (i7, 4.4 GHz) with a NVIDIA Quadro graphics card. The stimuli were presented using PsychToolbox (Brainard, 1997; Pelli, 1997) on a Sony Trinitron G520 monitor with a 60 Hz refresh rate and 1280 × 1024 pixels resolution. The observers viewed the monitor from a 70 cm distance, maintained with chin rest, resulting in the display subtending 32° × 25.75° and thus each pixel subtending 1.5’ × 1.5’. The luminance was gamma-corrected using a Cambridge Research System ColorCAL II photometer and custom-written software. The background of the monitor was set at a mid-gray with a luminance of 87.5 cd/m², and the maximum white luminance was set at 175 cd/m².

5.4.2.3 Stimuli and Procedure

The stimuli for the novel motion illusion consisted of an array of spatially
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separated Gabor-like elements (Movie 1). The envelopes (Eqn. 2) of the Gabors rigidly translated at 8°/sec for 400 ms behind a large circular aperture, centered 8.75° from fixation. The standard deviation of each Gaussian was 1° in height and 0.25° in width with a carrier spatial frequency of 2 c/° in the angular dependence experiment. The contrast of the Gabor was 100%. To give the appearance of a stimulus moving behind an aperture and to remove edge cues, a stationary 2D Gaussian weighting, with a 6.35° diameter, was used to modulate the luminance of the elements within it.

Movie 1. An example of the novel illusion showing that carrier orientation repels the perceived direction of the array. The demo shows a vertically-translating field of elongated Gabor-like elements. The orientation of the carrier is 30° from vertical.

Equation 2: The luminance profile (S) of the envelope for the Gabor-like elements used in the novel motion illusion.

\[
S(x, y) = \exp \left( -\frac{x^2}{2\pi\sigma_x^2} \right) \times \exp \left( -\frac{y^2}{2\pi\sigma_y^2} \right)
\]

The perceived direction of the field of Gabors is repelled from the carrier orientation at low spatial frequencies but attracted towards the carrier orientation at high spatial frequencies. The magnitude of the motion direction illusion was estimated using a Quest staircase procedure (Watson & Pelli, 1983). Interleaved staircases were run for 10 different Gabor carrier orientations (from 0° to 90° from vertical) to measure the
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angular dependence of the illusion. Whereas five interleaved staircases (0.25 c/°, .5 c/°, 1 c/°, 1.5 c/°, 2 c/°) were conducted for the carrier spatial frequency condition. Fixation was maintained with a centrally-presented point.

The observer indicated whether the stimulus moved to the left or right of vertical after each presentation. The true motion direction in each trial was given by the QuestMedian function in PsychToolbox. The point of subjective equality was taken as the 50% threshold given by the QuestMean function in PsychToolbox after 40 trials. No feedback was given following the responses. Two blocks were run for each condition for the observers.

5.5 Results and discussion

The manuscript begins by showing that the model predicts the angular dependence of an illusion where the orientation of Gabor-like element repels perceived direction of motion (Movie 1). To do this, we compared the model’s predictions against newly-collected psychophysical data (Figure 3). It is then shown that orientation can either attract and repel perceived motion direction depending on spatial frequency of the Gabor-like elements. The initial demonstration that orientation can either attract or repel perceived motion direction then provides a potential explanation for a number of existing illusions, previously discussed separately, using one simple model. The demonstration movies of the existing illusions have been constructed to use similar stimulus parameters as the original experiments to portray the reported effects.

Throughout the modeling section, the only free parameter was the gain relationship between the orientation and motion-selective neurons. The bandwidths of the model were held constant throughout the modeling. The differences in gain between experiments can mainly be attributed to contrast of the stimuli, or whether it was presented in central or peripheral vision, with differences in gain systematically increase
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in the periphery.

5.5.1 Orientation can repel or attract motion direction

The novel illusion shows that the perceived motion direction of a field of Gabor-like elements is repelled by the envelope orientation (Movie 1). Figure 3a shows the model predictions against the magnitude of the illusion when the orientation of the envelope was varied. The largest change in perceived direction occurs when the orientation is approximately 45° away from the veridical direction of motion. This is a similar tuning to the motion direction aftereffect (Schrater & Simoncelli, 1998) and approximately double that for the static tilt aftereffect (Dickinson, Almeida, Bell, & Badcock, 2010; Dickinson et al., 2012; O’Toole & Wenderoth, 1977), the tilt illusion (Wenderoth & Johnstone, 1988), and the Fraser illusion (Dickinson et al., 2012). This tuning suggests that it is unlikely that the observers were relying on orientation information alone, as this would cause narrower form-like tuning. The model provides a very good fit to the data.
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Figure 3. a. The model’s predictions for the orientation tuning of the newly-presented illusion. The circles indicate the data points and the line indicates the model’s predictions. b. The change in perceived direction as the carrier spatial frequency was varied. The dots have been joined with the line not indicating the model predictions. The error bars in all the panels represent ±1 standard error.

We next examined how varying the carrier spatial frequency affects the perceived motion direction (Figure 3b, Movie 2). The figure shows that the perceived direction of the array is repelled at low spatial frequency, but changes to being attracted at higher spatial frequencies. The model can explain why orientation either repels or attracts motion direction. The sensitivity of motion-selective neurons decreases when orientation-selective neurons feed inhibitory, but increases with excitatory, gain. Decreasing the sensitivity shifts the population response away from the orientation cue whereas the peak population response is attracted towards the orientation cue when sensitivity has been increased. Therefore, these results suggest that the gain relationship between orientation- and motion-selective neurons is dependent on spatial frequency.

The change in direction with spatial frequency is also consistent with a previous demonstration that motion is attracted to the orientation of a high spatial-frequency adapting Gabor and repelled from a low spatial-frequency adaptor (Tang et al., 2015). Furthermore, like the twisted cord illusion, the tilt aftereffect can be either attracted or
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repelled from the carrier orientation depending on the spatial frequency relationship (Dickinson et al., 2012; Skillen et al., 2002). Overall, it seems that this illusion is the form-motion equivalent of the tilt and twisted cord illusions as simultaneously-presented orientation attracts or repels perceived motion direction depending on the spatial frequency.

Movie 2. An example of the effect of varying the carrier’s spatial frequency for the novel form-motion illusion. As the spatial frequency increases the illusion changes from repulsion to attraction. The same 30° from vertical envelope orientation is used in each instance.

5.5.2 Background lines attract motion direction

Anstis (2012) provided a compelling illusion showing that the perceived direction of a dot is attracted towards the orientation of background lines (Movie 3). Anstis’ ‘furrow illusion’ shows two dots horizontally-translating across an oriented grating with the perceived directions appears attracted towards the orientation of the grating. Consistent with our argument about the importance in spatial frequency in determining whether orientation attracts or repels perceived direction, the perceived direction of moving dots can also be repelled by background lines when the spatial frequency relationship is different (Khuu, 2012). However, Khuu (2012) did not measure the orientation dependence of the illusion and has, therefore, not been included in the present manuscript.
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Movie 3. A demonstration of the effect of background lines on the perceived direction of two moving dots (Anstis, 2012). The perceived direction of the dots is attracted towards the lines. The effect is even more pronounced when the illusion is viewed in the periphery. Originally presented at http://jov.arvojournals.org/article.aspx?articleid=2191978.

The dot had the same width as the lines and moved horizontally at 12°/sec. The overall magnitude of the illusion was determined by the orientation difference between the dot’s direction and the background orientation predicted by the model (Figure 4). The largest direction attraction occurred when the orientation difference was around 50° which is slightly broader than the previous result where peak occur around 45°. Interestingly, the broader tuning of the effect appears to be due to the larger magnitude of perceived attraction. The large magnitude of the attraction is likely because the stimulus was presented 24° in the periphery, with the magnitude of the effect linearly increasing as the stimulus is moved away from central presentation (see Figure 1 in Anstis, 2012). Anstis (2012) argued that his ‘furrow illusion’ is different to the kinetic Zollner illusion (Khuu, 2012) because it is larger and was attractive rather than repulsive. However, we believe these are the same illusion as the furrow illusion is larger because the peripheral presentation and attractive because of the different spatial frequency relationship used in the experiments. Otherwise, like our novel illusion, the model would predict the same pattern of results for both the furrow and kinetic Zollner
illusions except that one is repulsive and the other attractive. A related illusion has been presented showing the perceived path of a horizontally-moving dot could either move in (showing attraction) or out of phase (showing repulsion) with a curved static path (Masson, Dodd, & Enns, 2009).

\[ \text{Figure 4.} \text{ The perceived direction of a translating dot is attracted to the orientated stripes (Anstis, 2012). } \]

The model’s predictions (lines) against the data (points). The error bars in all the panels represent ±1 standard error.

**5.5.3 Background lines repulsive motion direction**

The next presented illusion will show this predicted relationship for a repulsive effect of background lines on motion direction and it will be explained by the same form-motion mechanism. The perceived direction of a moving field of dots is repelled away from the veridical direction in the presence of an oriented static line (Braddick, Wishart, & Curran, 2002; Farrell-Whelan & Brooks, 2013; Farrell-Whelan, Wenderoth, & Brooks, 2012; Swanston, 1984). Farrell-Whelan and colleagues argued that static lines repelling perceived motion direction is a special case of the direction repulsion illusion generally caused with two motion planes (Marshak & Sekuler, 1979), because of the importance of non-object signals in determining motion direction. Like the previous illusion (Anstis, 2012), we argue that instead orientation simply modulates the gain of motion-selective neurons resulting in the direction shifts.
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**Movie 4.** A demonstration that a background line will repel the perceived direction of a field of moving dots (Farrell-Whelan & Brooks, 2013; Farrell-Whelan et al., 2012). The movie begins with a field of vertically translating dots. After 1 second, a background line is displayed which changes the perceived motion direction.

The magnitude of direction repulsion was measured for different line orientations in the original experiment (Figure 5). The observers adjusted the veridical motion direction so the dot field appeared to move vertically. Like the previous examples, the magnitude of perceived direction change is determined by the orientation of the lines relative to the motion direction. The model accurately predicts the orientation-dependence of the illusion. The authors explained the original result using a different model where direction is signaled through a comparison between velocity estimates of object and background motion (Dakin & Mareschal, 2000).
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**Figure 5.** The repulsive effect of background lines on motion direction from (Farrell-Whelan and Brooks, 2013). The model’s predictions (lines) are plotted against the results from the previous experiments (points). The error bars in all the panels represent ±1 standard error.

**5.5.4 Glass patterns attracted to orientation of pairs**

Randomly positioning appropriately-oriented dot pairs can give the vivid impression of static form consistent with the global pattern orientation, known as a Glass patterns (Glass, 1969; Glass & Pérez, 1973). If these patterns are rigidly moved, the perceived direction is attracted towards the orientation of the pairs (Ross, 2004, Movie 5). This illusion is, therefore, different to the previous two results, as the orientation information is an intrinsic property of the stimulus rather than being presented in the background. Similar to our argument, Ross (2004) stated that the reported direction attraction results from the orientation being detected by a motion streak-like mechanism that feeds into the stage of global motion processing.
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Movie 5. An example of the stimulus showing the direction of a translating glass pattern is attracted towards the pattern orientation (Ross, 2004). The orientation of the dot pairs gives the pattern orientation, in this case 30° from vertical. The actual motion direction is vertical but the pattern is perceived to be moving slightly leftwards.

The original study (Ross, 2004) varied the true motion direction for a number of different pattern orientations. The perceived motion direction was attracted towards the pattern orientation, with the magnitude of change dependent on the orientation (Figure 6). Our proposed model accurately predicts that the glass patterns with the dot pairs oriented at 25° cause a greater amount of direction attraction than when the dot pairs are oriented at 65°. Again, this suggests that orientation can directly modulate motion direction processing at the stage of global motion processing in the proposed manner.
Figure 6. The effect of the orientation of the dot pairs in translating Glass pattern on the perceived motion direction from (Ross, 2004). The model’s predictions (lines) provide a good fit for the data (points). The error bars represent ±1 standard error.

During the construction of the demonstration for Movie 5, it was found that the perceived direction of motion could also be repelled from the pattern orientation (Movie 6). We changed the luminance profile of the dots from hard edged with a square-wave function to a fourth derivative of a Gaussian function. This manipulation constrains the spatial frequency to be ~7 c/°, rather than the broadband profile for the dots with a box-car luminance profile. This is further support for the idea that orientation can either attract or repel perceived motion direction depending on the spatial-frequency relationship.
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Movie 6. An example of the stimulus showing the direction of a translating glass pattern is repelled away from the pattern orientation. The luminance profile of the dots has been changed from a hard edge box-car function in Movie 5 to a 4th derivative of a Gaussian function, which constrains the spatial frequency.

5.5.5 Orientation disambiguates the Barber Pole illusion

The barber pole illusion shows the effect of orientation on ambiguous motion signals, which are subject to the aperture problem. The classic version of the illusion shows a grating drifting within a vertically-elongated aperture. The direction is always perceived to move vertically regardless of the carrier orientation (Wallach, 1935). However, later studies have revealed that the perceived direction follows the local orientation information of the aperture (Movie 7; Badcock et al., 2003; Kooi, 1993). Furthermore, merely placing abutting oriented lines beside a regular elongated aperture attracts the perceived motion direction towards the line orientation (Badcock et al., 2003). This suggests that orientation information directly changes motion representations of ambiguous motion. The original explanation argued that a motion-streak mechanism could cause orientation to have this effect on ambiguous motion (Badcock et al., 2003).
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Movie 7. A demonstration that the perceived motion direction for the Barber pole illusion is determined by the orientation of the aperture. The example is slightly different to the previous results as the motion signal is consistent with any direction within 180° (i.e. were subject to the aperture problem) whereas the motion signals in previous examples provided a 2D vector.

This illusion is, however, different to the previously discussed form-motion effects, which resulted from motion estimates not subject to the aperture problem. While motion signals in the previous illusions have been treated as resolved 2D vectors, the motion in the barber pole illusion could, however, represent any motion direction within 180° but with different velocities. To account for this, the model could be modified to produce a motion response subject to the aperture problem (Adelson & Movshon, 1982). But in the current model, increasing the gain from the orientation-selective channels to the motion-selective channels most easily represents this. When this is done, the model predicts that orientation attracts the perceived motion direction because orientation increases the sensitivity of motion-selective neurons along the corresponding axis.
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![Graph](image)

**Figure 7.** The change in perceived direction of the barber pole illusion when the local orientation of the elongated aperture changes from Badcock et al. (2003). The model’s predictions (lines) provide a good fit for the data (points). The error bars in all the panels represent ±1 standard error.

### 5.6 Conclusions

The current study has provided strong evidence that orientation directly influences motion processing at the stage of global motion integration. This is contrary to the prominent theories, both psychophysical and neurophysiological, of motion processing which commonly argue that form and motion are processed independently (Braddick et al., 2000; Livingstone & Hubel, 1987; Mishkin et al., 1983). A novel mechanism where narrowly-tuned orientation-selective neurons directly influence broadly-tuned motion-selective neurons at a later stage was proposed. The mechanism uses well-established gain control to modulate the activity in separate banks of neurons (Carandini & Heeger, 2012; Heeger et al., 1992). The gain control mechanism allows the system to be self-calibrating adapting to statistics in the natural environment (Ullman & Shechtman, 1982). This interaction between orientation and motion neurons causes the shape of a moving object to influence its perceived direction. We found that this model could describe the results of a number of psychophysical illusions that had mainly been attributed to other, more complicated, factors.
One of the most interesting findings of the present work is that motion can either be attracted or repulsed by the orientation depending on the spatial frequency relationship. This bi-directional influence of orientation on perceived motion direction allows a number of separate illusions to be attributed to the same process and provides a novel insight into visual processing. We have previously shown that the perceived direction following adaptation to static form is dependent on spatial frequency (Tang et al., 2015). The effects that we have described could be considered analogous examples to the tilt illusion (O'Toole & Wenderoth, 1977), which shows a similar spatial frequency dependency (Dickinson et al., 2012; Skillen et al., 2002). The orientation repulsion in the tilt illusion can be accounted for by the reduced neuronal responses to the orientations of the contextual elements. The current results showing our proposed model predicts many instances of orientation affecting perceived motion direction suggest that it is likely there are corresponding changes in the responsiveness for both form- and motion-sensitive neurons.

A similar mechanism has been proposed to explain the tilt illusion, where perceived orientation is influenced by the surrounding orientation, which could be considered the static equivalent of the results reported here (Clifford, 2002, 2014). The impact of orientation on perceived motion direction linearly increases with presentation eccentricity (Anstis, 2012; Cormack, Blake, & Hiris, 1992). The magnitude of tilt aftereffects also increase when measured in the periphery compared with central presentation (Dickinson et al., 2012). Likewise, decreasing the contrast of the tested stimulus systemically increases the magnitude of aftereffects (Keck et al., 1976).

The model suggests that orientation information modulates the sensitivity of broadly-tuned motion-sensitive neurons, most likely at the stage of global motion integration. Orientation information from V1 seems likely to input directly into V5 as
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this area receives most of its inputs from V1 (Born & Bradley, 2005). It is, therefore, possible that the proposed form-motion model is instantiated from an interaction between neurons in V1 and V5. However, there are also direct connections between V5 and V4, which is strongly associated with form processing (Desimone & Schein, 1987; Felleman & Van Essen, 1991; Maunsell & van Essen, 1983; Ungerleider, Galkin, Desimone, & Gattass, 2008). V4 itself contains a direction preference map that could be another site for form-motion interactions (Li et al., 2013). Regardless of the neurophysiological implementation, the main thrust of the current study is to suggest that two separate banks of neurons, one selective for orientation, the other form, interact.

Neurophysiological studies would need to be conducted to determine the exact neural locus of the proposed interaction. Presenting a series of locally uncorrelated patterns but with a consistent global pattern give the impression of motion along the global pattern orientation, known as dynamic Glass patterns (Ross et al., 2000). The form information contained within these patterns strongly activates human V4 (Mannion, Kersten, & Olman, 2013) while dynamic versions produce strong activation in monkey STS (Krekelberg, Dannenberg, Hoffmann, Bremmer, & Ross, 2003) and human V5 (Krekelberg, Vatakis, & Kourtzi, 2005). These results could be consistent with our recent demonstration that form information enters the motion system by, at least, the stage of global motion integration (Tang, Dickinson, Visser, Edwards, & Badcock, 2013). The form information could influence motion processing at the stage of motion integration directly from V1, as suggested by the current model or through higher-level specialized form areas.

The proposed simple constraint on motion processing by orientation signals could explain a large number of previously-described form-motion interactions.
Oriented form cues, caused by the extended integration time of V1 neurons, improve motion sensitivity (Apthorp et al., 2013; Edwards and Crane, 2007; Geisler, 1999; Geisler et al., 2001). Humans are also extraordinarily sensitive to biological motion given by the spatial arrangement, and the trajectories, of a field of independently moving dots (Blake and Shiffrar, 2006; Johansson, 1973, 1976). Perception for biological motion remains intact despite lesions to regions in the ventral stream (Gilaie-Dotan, Bentin, Harel, Rees, & Saygin, 2011), but strongly activates global motion areas (MST, V5; Beauchamp, Lee, Haxby, & Martin, 2003). This could suggest that our model for orientation-selective neurons modulating motion-selective neurons could provide a mechanism that allows human’s acute sensitivity to biological motion.

The visual system may also use form information to determine which motion signals to integrate (Lorenceau & Alais, 2001; Lorenceau & Lalanne, 2008; Lorenceau & Shiffrar, 1992). This form information allows the system to overcome the separation between first and second-order motion (Maruya & Nishida, 2010), generally not thought to be integrated until after the stage of global motion integration (Cassanello, Edwards, Badcock, & Nishida, 2011; Edwards & Badcock, 1995). Finally, form changes can also give the impression of motion in the direction that explains the shape change regardless of the low-level motion signals (Tang et al., 2013; Tse & Caplovitz, 2006; Tse, Cavanagh, & Nakayama, 1998; Tse & Logothetis, 2002). All these form-motion interactions could possibly be underpinned by our proposed mechanism where orientation is detected in an early stage of the processing hierarchy then enters the motion system at the stage of global pooling.

Overall, the current study has provided evidence that orientation information directly modulates motion processing at the stage of global motion pooling. The novel contribution of the study is to show that an object’s shape will change its perceived
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motion direction. We have shown that one model that allows a simple constraint of broadly-tuned motion selective neurons by narrowly-tuned orientation-selective neurons can potentially explain a number of existing form-motion illusions. These results importantly suggest that orientation information constrains motion processing in a manner unaccounted for by existing models of visual processing and, therefore, must be considered when determining motion direction.

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5.8 References


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6 The role of form information in motion pooling and segmentation


1. School of Psychology, The University of Western Australia, Crawley, WA, Australia
2. Research School of Psychology, The Australian National University, Canberra, ACT, Australia

6.1 Foreword

One of the key challenges for the visual system is overcoming ambiguity in the representation of motion information in early visual cortex. The small size of neurons in V1 which can only resolve a small portion of each object and thus also its motion, meaning that each neuron produces a motion signal consistent with any direction within a 180° arc in response to an elongated contour (Adelson and Movshon, 1982). Combining many early signals together using various computational strategies (intersection of constraints, vector averaging, harmonic vector averaging) can solve this ambiguity. The solution to this aperture problem is further complicated as scenes often contain either multiple moving objects or self-induced motion causing most objects to generate motion signals relative to the observer. This means that each set of directionally-ambiguous motion signals belonging to one object must be integrated, while being segmented from those signals belonging to other objects. Form information which would definitively indicate which set of signals belong to each object, is rarely considered for solutions of the aperture problem.

The four previous experimental chapters have shown that form information can enter the motion system by, at least, the stage of global motion integration (Chapter 1) and that this information can influence perceived motion direction (Chapters 3-5). These findings suggest that form information is, at least, available, by the stage that low-level motion signals are integrated, meaning that form information could be used in the integration/segmentation problem caused by multiple, moving objects. A class of stimulus, which will be referred to as the ‘occluded aperture’ stimuli, has suggested that form information does affect the segmentation or integration of motion signals (Lorenceau & Alais, 2001; Lorenceau & Lalanne, 2008; Lorenceau & Shiffrar, 1992;
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McDermott & Adelson, 2004; McDermott, Weiss, & Adelson, 2001; Shiffrar & Lorenceau, 1996). This stimulus shows a diamond rotating behind four stationary apertures, which gives the impression of either two opposing lines translating (showing segmentation) or a full diamond rotating (showing integration).

The contour information from the diamond appears to be important for determining the change between segmentation and integration. A shape forming an open contour causes segmentation in conditions that would cause a closed contour shape to be integrated. This suggests that the form information may be being used for determining integration and segmentation. However, the exact mechanism of how form information affects motion pooling in this stimulus has yet to be fully elucidated. The next chapter will show what conditions cause the change between integration and segmentation as well as showing the role of form information in this process. The results in the study suggest that the resolution of low-level motion signals determine whether the occluded-aperture stimuli are integrated or segmented. Segmentation occurs in condition of low stimulus noise, which allow for multiple motion directions to be independently resolved. Integration, however, occurs in conditions of higher noise, where multiple motion signals cannot be resolved. The results also suggest that the presence of a closed contour does not increase global motion sensitivity relative to condition without extended contour information.

References

6.2 Abstract

Traditional theories of visual perception have focused on either form or motion processing, implying a functional separation. However, increasing evidence indicates that these features interact at early stages of visual processing. The current study examined a well-known form-motion interaction, where a shape translates along a circular path behind opaque apertures, giving the impression of either independently translating lines (segmentation) or a globally coherent, translating shape. The purpose was to systemically examine how low-level motion information and form information interact to determine which percept is reported. To this end, we used a stimulus with boundaries comprising multiple, spatially-separated Gabor patches with three to eight sides. Results showed that shapes with four or fewer sides appeared to move in a segmented manner, whereas those with more sides were integrated as a solid shape. The separation between directions, rather than the total number of sides causes this switch between integrated or segmented percepts. We conclude that the change between integration and segmentation depends on whether local motion directions can be independently resolved. We also reconcile previous results on the influence of shape closure on motion integration: shapes that form open contours cause segmentation, but with no corresponding enhanced sensitivity for shapes forming closed contours. Overall, our results suggest that the resolution of the local motion signal determines whether motion segmentation or integration is perceived with only a small overall influence of form.
6.3 Introduction

One of the key challenges for the visual system is the correct assignment of motion signals to corresponding objects. This task is complicated by the small size of receptive fields of neurons in V1, which cause extended moving contours to produce ambiguous responses, consistent with any direction within a 180° arc (Adelson & Bergen, 1985; Adelson & Movshon, 1982; Amano, Edwards, Badcock, & Nishida, 2009a; Nishida, 2011). The visual system must use this limited information to decide which signals should be integrated to represent one object and which should be segmented to represent multiple objects. Further, form information, which could definitively indicate the objects generating each set of motion signals, is rarely considered to be involved in this task as the conventional view suggests that form and motion are functionally independent (Braddick, O’Brien, Wattam-Bell, Atkinson, & Turner, 2000; Livingstone & Hubel, 1987; Mishkin, Ungerleider, & Macko, 1983).

In contrast to this conventional view, there is now considerable evidence showing that form information can affect motion processing at early stages of processing. For example, the vivid impression of a moving human or animal can be given by a small number of moving dots (Johansson, 1973, 1976). Additionally, motion streaks, caused by the extended integration time of V1 neurons (Geisler, 1999), increase sensitivity to global motion detection (Apthorp et al., 2013; Edwards & Crane, 2007) and influence perceived direction (Ross, Badcock, & Hayes, 2000; Tang, Dickinson, Visser, & Badcock, 2015). Presenting a series of locally-uncorrelated patterns but with a globally-consistent pattern results in the perception of motion in the global pattern direction, likely through activation of the motion streak mechanism (Badcock & Dickinson, 2009; Burr & Ross, 2002; Dickinson & Badcock, 2009; Ross et al., 2000). Adding explicit hard edges to Gabors pulls the perceived direction of motion towards...
the orientation cue (Badcock, McKendrick, & Ma-Wyatt, 2003; Edwards, Cassanello, Badcock, & Nishida, 2013), and form changes, without a corresponding motion energy signal, can be pooled into a global motion percept (Tang, Dickinson, Visser, Edwards, & Badcock, 2013; Tse, 2006). Taken together these studies suggest that form information enters the motion system by, at least, the stage of global motion integration and that this information can assist in the recovery of object motion direction.

6.3.1 The occluded-aperture stimulus

The current study sought to determine how form information assists in the pooling of motion information because form information would both aid integration/segmentation processes and appears to be available to the visual system at an early stage of processing. To examine this question, we used an occluded-aperture stimulus has been extensively used to examine how form information apparently affects which motion signals are integrated or segmented (Movie 1). The stimulus, first described by Lorenceau and Shiffrar (1992), which consists of a diamond translating on a circular path behind four stationary apertures (see Movie 1). This stimulus produces either a vivid impression of one object globally translating in a circle (showing integration) or two pairs of opposing bars together translating perpendicular to the contour (showing segmentation) depending on the stimulus configuration.
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**Movie 1:** Two examples of occluded-aperture stimuli. **Left panel:** A stimulus configuration leading to motion segmentation, where the opposing line pairs are perceived as translating perpendicularly to the contour. **Right panel:** A stimulus configuration leading to motion integration with visible occluders. The square can generally be seen to be translating in an anti-clockwise direction.

There have now been a substantial number of descriptions of the stimulus configurations that change the percept for the occluded-aperture stimulus from segmented to integrated (Caclin et al., 2012; Kane, Bex, & Dakin, 2011; Kane, Bex, & Dakin, 2009; Lorenceau & Alais, 2001; Lorenceau & Lalanne, 2008; Maruya & Nishida, 2010; McDermott & Adelson, 2004; McDermott, Weiss, & Adelson, 2001; Shiffrar & Lorenceau, 1996), with many claiming to demonstrate that form constrains motion integration. However, many of these results could be explained by low-level mechanisms without any reference to global form information. For instance, presenting the stimulus in the periphery (Lorenceau & Alais, 2001), at low contrasts (Lorenceau & Alais, 2001; Shiffrar & Lorenceau, 1996), or for short durations (Shiffrar & Lorenceau, 1996) makes the percept switch from segmented to integrated. However, Lorenceau and Alais (2001) have argued these results reflect degradation of the parvocellular input which provides form information to the motion system.
6.3.2 Low-level motion information

These manipulations, however, also cause the percept for conventional motion stimuli (plaids, multi-aperture pseudo-plaids) to change from transparent to integrated (Kim & Wilson, 1993, 1996; Takeuchi, 1998). This change between integration and transparency has been explained without reference to form information; instead, it has been argued that the representation of low-level motion information is the crucial variable. Transparency is thought be perceived because each direction produces a distinct population response whereas degrading the representations causes overlapping responses, creating the need to integrate directions using intersection of constraints (IOC) or vector averaging rules (Qian & Andersen, 1994). Such arguments suggest that, in at least some instances (Lorenceau & Alais, 2001; Shiffrar & Lorenceau, 1996), the change in percept for the occluded-aperture stimulus can be explained by the motion representation without reference to form information.

Taking this possibility as a jumping off point, an analysis of the parameters of the occluded-aperture stimulus suggests other potential avenues for examining the role of motion representations in determining the resulting percept. For example, to our knowledge, all previous occluded-aperture studies have used a four-sided stimulus. This configuration causes the bars to have one of two motion directions, with each direction separated by 90° (Figure 1). For stimuli without form information (i.e. plaids), transparency and integration are equally likely to be perceived when the component directions are separated by 90°, with integration frequently occurring with less, and transparency occurring with greater, directional separations (Alais, van der Smagt, Van den Berg, & Van de Grind, 1998; Kim & Wilson, 1993). These results can be understood in the framework mentioned above, with the population response more likely to cause overlap when the directional separation are decreased. If the change in
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percept for the occluded-aperture stimulus is governed by the low-level motion representation, then decreasing the direction separation should increase motion integration. This could be accomplished by increasing the number of sides, while retaining the closed contour information.

**Figure 1**: A schematic example of a diamond (four-sided) version of the occluded aperture stimuli (a) and the associated speed of each contour which are subject to the aperture problem (b). Panel b shows the relative velocities of the contours needed to produce circular translational motion. The lines in (b) correspond in color to each side in (a). The opposing pairs of bars have identical motion because the velocity is given by the cosine of the difference of the global motion direction and contour orientation.

An additional issue arises from the previous studies having also used stimuli with a broad spatial-frequency profile. The orientation bandwidths of motion-selective neurons linearly increase with increasing spatial frequency (Anderson & Burr, 1985; De Valois, Albrecht, & Thorell, 1982). The population response would be much broader (and more likely to overlap) when spatial frequency increases. Therefore, if the occluded-aperture stimulus is governed by the representation of the motion signal then integration should increase when spatial frequency also increases.

### 6.3.3 Global form information

So far, we have argued that the change in percept for the occluded-aperture stimulus may result from the representation of low-level motion information. We believe this because many of the same manipulations that cause motion stimuli without global form cues to change from transparent to integrated also cause corresponding effects in the occluded-aperture stimuli (Kim & Wilson, 1993, 1996; Lorenceau &
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Alais, 2001; Shiffrar & Lorenceau, 1996; Takeuchi, 1998). Some evidence arising from the use of the occluded-aperture stimulus does, however, suggest that form information may provide a global constraint for motion integration.

An influential study found that integration occurs for occluded-aperture stimuli forming closed contours (diamonds) but not when they form an open contour (crosses), even though both stimuli have elements carrying identical low-level information, including the same directional separation and spatial frequency (Lorenceau & Alais, 2001). This finding can be interpreted in light of the visual system’s Gestalt-like preference for shapes forming closed contours (Wagemans et al., 2012). However, this result has been recently challenged by a demonstration showing that motion stimuli presented behind many apertures can be integrated without a closed contour configuration (Kane et al., 2011; Kane et al., 2009). There is, therefore, conflict in the literature about the necessity of shape information for the occluded-aperture stimulus. An associated issue for this finding is whether closed contours enhance integration or only veto motion integration. This is because no study has used an occluded-aperture stimulus where the same motion information can be presented with or without global form information.

6.3.4 Current aims

The current study sought to overcome the identified limitations in the occluded-aperture literature by looking at two sets of related questions. The first section examined how low-level motion information affects the percepts for the stimulus (Experiments 1-5). The second looked at how global form information, from closed and open extended contours, constrains motion integration (Experiments 6-7). We examined these questions by constructing a novel, multi-aperture version of the occluded diamond stimulus where the contour was made from multiple Gabors (Movie 2). This stimulus
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allowed us to have a broad distribution of motion signals where we could vary the
directional separation, control for spatial frequency and separately manipulate form and
motion information. Furthermore, the stimulus also allowed us to carefully vary the
number of motion signals consistent with the 2D global direction, analogously to
standard global motion tasks, whereas most previous studies just asked participants to
report whether the stimulus appears coherent.

Movie 2: Examples of the occluded-aperture stimuli with the number of sides increasing from three to
eight. In each presentation there is true clockwise translation along a circular path. The number of sides
did not change within an experimental trial. This stimuli shows the 2 c/° condition in Experiment 1.

Specifically, our initial experiments (1-5) addressed whether the representation
of the population response is responsible for the change in percept by increasing the
number of sides (decreasing direction separation) and spatial frequency in the occluded-
aperture stimulus. Later experiments expand this line of enquiry by separating number
of sides and orientations by varying only the carrier orientation of the Gabor while
keeping the number of sides constant. Experiment 5 sought to link the different percepts
of the occluded-aperture stimulus with conventional motion stimuli. Later experiments
(6-7) sought to reconcile the seemingly conflicting recent results about the necessity of
the occluded shapes forming closed contours for motion integration (Kane et al., 2011;
Kane et al., 2009; Lorenceau & Alais, 2001). To address this uncertainty, motion
integration for shapes, forming either closed or open contours, was compared to stimuli without extended overall form information.

6.4 General methods

6.4.1 Observers

Four experienced observers, between the ages of 24 and 50 years (median = 29 years), took part in the study, with three observers participating in each experiment. Two of the observers were authors, while the others were naïve to the experimental aims. All observers had normal or corrected-to-normal visual acuity as assessed using a LogMAR chart. The procedure was in accordance with the Declaration of Helsinki and approved by the Human Research Ethics Committee at the University of Western Australia with observers providing written, informed consent.

6.4.2 Apparatus

The stimuli were generated in MATLAB 8.1 on a PC running OS X 10.9 (i7, 4.4 GHz) with a NVIDIA Quadro graphics card using PsychToolbox 3 (Brainard, 1997; Pelli, 1997). The stimuli were displayed on a Sony Trinitron G520 monitor with a 60 Hz refresh rate and a 1280 × 1024 pixel resolution. A Cambridge Research System Bits# system was used to achieve 14-bit gray scale resolution. The observers viewed the monitor from 70 cm, maintained with a chin rest, resulting in the display subtending 32° × 25.75° and thus each pixel had a subtense of 1.5’ × 1.5’. The luminance response of the monitor was gamma-corrected using a Cambridge Research System ColorCAL II photometer and custom-written software. The background of the monitor was set at a mid-gray with a luminance of 87.5 cd/m², and the maximum white luminance was set at 175 cd/m².
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6.4.3 Stimuli

The stimuli were based on previous experiments using occluded-aperture designs (Lorenceau & Alais, 2001; Lorenceau & Shiffrar, 1992; McDermott & Adelson, 2004; McDermott et al., 2001). The shapes were regular, equiangular polygons that varied between having three and eight sides depending on the condition (Movie 2). The boundary contours of the shapes were made from sets of Gabor's so that spatial frequency and orientation content could be manipulated. To make the shape appear to move, the drift rates of the carriers of the Gabor's were made to be consistent with an IOC global motion of translation along a circular path, while the envelope remained stationary (Amano et al., 2009a; De Valois & De Valois, 1991). The IOC-defined drift rates were given by the cosine of the difference between the Gabor orientation and the desired global direction. The shape was made to appear occluded by not placing Gabor's near the corners and, thus, each side was always a straight line. Unless noted, the Gabor's had an envelope standard deviation of 0.06° and were presented at 100% contrast. The number of Gabor's on each side of the shape was varied so there were always 60 Gabor's in total (except in Experiment 2 where there were 40). Unless noted, the orientations of the carriers in each Gabor were parallel to the orientation of the side that contained it. On each trial, the starting position of the circle defining the 2D motion direction was randomized to minimize observers using the initial directions of each contour to judge the global direction.

6.4.4 Procedure

Each trial began with a stationary version of a stimulus, surrounding a centrally-presented fixation dot. After 400 ms, the carriers of the Gabor's drifted at the globally-assigned rate for 400 ms, before the stimulus disappeared. The observers were required to indicate whether the shape appeared to move clockwise or anti-clockwise.
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Analogously to studies measuring motion sensitivity using the Global Gabor array (Amano et al., 2009a; Cassanello, Edwards, Badcock, & Nishida, 2011; Edwards et al., 2013), the number of total Gabors having drift rates consistent with the 2D global vector was varied, with the remainder assigned random drift rates. The Quest method (Watson & Pelli, 1983), implemented using in-built functions in PsychToolbox (Brainard, 1997; Pelli, 1997), controlled the staircase, with the QuestQuantile function giving the coherence level for each trial. Each staircase lasted for 30 trials and the 75% threshold was defined as the result of the QuestMean function after the 30th trial. Staircases for each stimulus condition (i.e. number of sides but not spatial frequency) were interleaved and completed in a pseudo-randomized order within each block. Observers completed three blocks of trials for each stimulus condition, with the threshold taken as the mean of the blocks.

6.5 Results and Discussion

6.5.1 Experiment 1: Varying number of sides

All previous studies, to our knowledge, that used the occluded-aperture have used a four-sided stimulus with a broad spatial frequency profile (Lorenceau & Alais, 2001; Lorenceau & Shiffrar, 1992; Maruya & Nishida, 2010; McDermott & Adelson, 2004; McDermott et al., 2001; Shiffrar & Lorenceau, 1996). This stimulus configuration causes the motion directions to be separated by 90° which is the point of equality between transparency and integration for motion stimuli without global form information (Alais et al., 1998; Kim & Wilson, 1993).

The current study investigated whether direction separation affects the percepts for the occluded-aperture stimulus by varying the number of sides of the polygon from three (a triangle; 120° of separation) to eight (an octagon; 45° of separation) in different experimental condition. We simultaneously examined whether spatial frequency affects
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introduction. Movies 2 and 3 show examples of the stimuli used. As can be seen in the low-spatial frequency examples in Movie 2, incoherent motion dominates when the polygon only has three or four sides. Each side appears to independently translate perpendicular to its contour, with no sense of global circular translational motion, showing the segmented percept. However, when there are more than four sides, the shape appears to coherently rotate as a single object, showing the integrated percept. At higher spatial frequencies of the carrier grating, the shape is always seen to rotate coherently regardless of the number of sides (Movie 3).

**Movie 3:** An example of the stimulus used in the 6 c/° condition in Experiment 1. In each presentation there is true clockwise circular translational motion. The number of sides of the polygon is varied between three and eight.

The coherence thresholds for determining whether the shape was rotating in a clockwise or anti-clockwise direction reflected the same pattern of results as the demonstrations (Figure 2). Coherence thresholds are very high (> 80%) when the percept is segmented, as the observers could not determine the global motion direction, and thus performed at chance levels. Motion integration was enhanced when observers perceived global rotation, leading to significantly lower thresholds (<50%).
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**Figure 2:** Motion coherence thresholds (75%) for detecting directions of global motion in Experiment 1. The number of sides of the polygon was varied and the spatial frequency of the Gabor s making up the contour boundary. The error bars represent ± 1 standard error.

These thresholds were subjected to a 6 (number of sides) × 3 (spatial frequency) repeated-measures ANOVA which supported this account of the pattern of results. There was a significant main effect of number of sides, $F(5, 10) = 5.59, p = .01$, $\eta_p^2 = .26$, and a marginal main effect of spatial frequency, $F(2, 4) = 5.04, p = .08, \eta_p^2 = .12$. Critically, there was also a significant interaction between number of sides and spatial frequency, $F(10, 20) = 3.05, p = .02, \eta_p^2 = .28$, which was followed up with post-hoc comparisons (with Bonferroni corrections) within each spatial frequency condition, comparing thresholds to the three-sided stimuli. This analysis showed for the 2 c/° condition, thresholds were significantly different for three sides versus more than four sides (all $ps < .05$), but not between three and four. But, for the 4 c/° and 6 c/° conditions, thresholds did not change with increasing number of sides (all $ps > .05$). This shows that thresholds decreased with increasing number of sides for the 2 c/°, but not 4 c/° or 6 c/° conditions. Motion integration occurs when the stimulus has more than four sides, or is presented at higher spatial frequencies. Otherwise, the stimulus is perceived as segmented leading to high thresholds because of motion segmentation.
6.5.2 Experiment 2: Controlling for number of cycles in each patch

Experiment 1 suggests that stimuli are much more likely to be perceived as integrated at higher spatial frequencies. However, an alternative possibility is that increased integration could be due to the higher spatial frequency stimuli having more cycles in each patch, rather than an effect of absolute spatial frequency. To test this possibility, the size of each Gabor along the path was doubled while the spatial frequency was kept constant at 2 c/° (Movie 4). This manipulation meant the number of cycles in each patch was doubled compared to the 2 c/° condition in Experiment 1 but the same as the 4 c/° condition. The total number of Gabors was reduced from 60 to 40 because the size of each was doubled.

Movie 4: An example of the stimuli used in Experiment 2 to determine whether the spatial frequency or number of cycles in each patch governed motion integration. The size of each Gabor was doubled compared to Experiment 1 while the spatial frequency was kept constant at 2 c/°.

The motion coherence thresholds for these stimuli were compared to the results to the 2 c/° condition in Experiment 1 (Figure 3). As the figure shows, thresholds for both small (from Experiment 1) and large Gabor patch sizes similarly decrease with increasing number of sides. A 6 (number of sides) × 2 (Gabor size) repeated-measures ANOVA supported this observation with thresholds not significantly differing for the
two patch sizes, $F(1, 2) = 0.03, p = .62, \eta_p^2 = .002$. Thresholds significantly decreased with increasing number of sides, $F(5, 10) = 3.36, p = .049, \eta_p^2 = .57$, and there was no significant interaction between factors, $F(5, 10) = 2.42, p = .11, \eta_p^2 = .02$. This strongly suggests the increased motion integration for higher spatial frequency stimuli was due to the spatial frequency rather than the number of cycles in each patch.

![Figure 3](image-url)

**Figure 3**: Motion coherence thresholds (75%) for the control condition in Experiment 2. The Gabors had standard deviation of $0.1276^\circ$ and a spatial frequency of $2 \text{ c/}^\circ$. The error bars represent $\pm 1$ standard error.

Furthermore, there does not appear to be any effect of total number of cycles on thresholds. In Experiment 1, the entire stimulus contained ~30 cycles whereas the stimulus in Experiment 2 contained ~40 cycles, but thresholds were comparable between these conditions. Later, in Experiment 5, it is shown that the increased motion integration with increasing spatial frequency is due to the manipulation also decreasing motion transparency limits. We believe this is because the orientation bandwidth, which allows for different motion directions to be independently resolved, linearly increases with spatial frequency (Anderson & Burr, 1985; De Valois et al., 1982).

### 6.5.3 Experiment 3: The number of directions and spatial frequency are critical for pooling

The results so far suggest that the occluded-aperture stimulus is only integrated
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when it is presented at lower spatial frequencies, and when the shape has more than four sides. The rationale for increasing the number of sides was to decrease the directional separation, which has previously been shown to be a critical variable for motion transparency and integration with motion stimuli without global form information (Alais et al., 1998; Kim & Wilson, 1993). Consistent with this hypothesis, our results show that motion integration increases as the directional separation decreases.

The next experiment separately manipulated motion direction separation and number of sides to elucidate the factor that causes the percept to change from segmented to integrated. To do this, we compared global motion thresholds for a triangle with one or two local element orientations/directions in each side (Movie 5). This triangle with two element orientations in each side has the same number of sides as the standard triangle, which was not previously integrated, but the same number of orientations (and directional separation) as the hexagon, which is integrated. Consistent with previous observations, the movie shows that the triangle is segmented when each side has one orientation. The triangle, however, gives a clear percept of global motion there are two orientations in each side. To confirm the results from Experiment 1, where integration increases with spatial frequency, we also included a higher spatial frequency condition. Observers could see the global motion direction in this condition regardless of the number of orientations in each side.
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**Movie 5:** An example of the stimuli in Experiment 3. In the first example, the shape is triangle with all the Gabors aligned along the contour, which is the same as the used in earlier experiments. In the second example, there are two local element orientations (each 22.5° from aligned along the contour) represented in each side.

The same pattern of results was observed for the measured global coherence thresholds for triangles with one and two orientations in each side (Figure 4). A 2 (orientation in each sides) × 2 (spatial frequency) repeated-measures ANOVA showed that thresholds significantly decreased with increasing number of orientations, $F(1, 2) = 27.84, p = .03, \eta_p^2 = .30$. There was no main effect of spatial frequency, $F(1, 2) = 7.42, p = .11, \eta_p^2 = .13$, nor a significant interaction, $F(1, 2) = 5.50, p = .14, \eta_p^2 = .34$. This result shows that number of orientations (coinciding with separation between directions) in the shapes determines whether it is integrated or segmented rather than the number of sides being the critical variable.
6.5.4 Experiment 4: Varying orientation in each side

Experiment 4 sought to build upon the previous result, where the number of orientations (and 1D directions) in each side determines motion integration. Experiment 3 used a constant orientation separation whereas the next experiment addresses the orientation separation necessary for integration. To do this, we used a three-sided occluded-aperture stimulus (a triangle) with a varying orientation range within each side (Movie 6). The orientations of the Gabors along each side of the triangle were allowed to vary by a set amount from parallel to the orientation of the contour. For example, the orientations of the individual Gabors were randomly varied between -20° and +20° from parallel to the contour when the orientation range was 40°. The drift rates were appropriately adjusted to maintain the 2D global circular motion. Movie 3 begins with the same triangle stimulus that was used in Experiments 1 and 2 with all the Gabors aligned parallel to the contour. The orientation range is increased in each subsequent presentation of the stimulus, with the orientation range in the last presentation being 180°. The movie clearly shows that segmentation is perceived when the orientation...
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range is small whereas the stimulus integrates when the orientation range is large.

Movie 6: An example of the stimuli used in Experiment 4 where the range of orientations of the Gabors was varied from aligned along the contour (0°) to completely randomized (180°). During the experiment, the orientation range during each trial was consistent.

We quantified the effect of increasing the orientation range on motion integration of the occluded triangle stimulus. Motion coherence thresholds were measured for six different orientation range conditions (0°, 20°, 40°, 60°, 120°, 180°) in an interleaved staircase procedure (Figure 5). We included two spatial frequency conditions (2 c/° and 6 c/°) to generalize the previous results showing differential integration depending on spatial frequency. Consistent with the previous results, motion integration is poor in 2 c/° condition when the Gabors are aligned along the contour. But, when the orientation range exceeds ~45° the triangle is more strongly integrated. Also consistent with the previous results, the triangle in the 6 c/° condition is equivalently integrated regardless of the orientation range.
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We compared the thresholds in this experiment using a 6 (orientation range) × 2 (spatial frequency) repeated-measures ANOVA. Thresholds decreased with increasing orientation range for the 2 c/° but not, 6 c/°, condition as evidenced by a significant interaction, $F(5, 10) = 4.16, p = .02, \eta_p^2 = .27$. Thresholds were also on average higher for the 2 c/° than 6 c/° condition, $F(1, 2) = 25.55 p = .03, \eta_p^2 = .19$. Because of the significant interaction, there was no main effect of orientation range, $F(5, 10) = 2.24, p = .13, \eta_p^2 = .17$. Follow-test, post-hoc test (with Bonferroni corrections) showed the spatial frequency conditions (2 vs. 6 c/°) were different with 0° and 20° orientation ranges (all $ps < .05$), but were statistically indistinguishable at larger ranges (all $ps > .05$). The crucial variable for determining whether the occluded shapes are globally integrated appears to be whether a critical range of orientations (>40°) is represented in the shape. This orientation range is similar to the orientation dependency of motion integration for a plaid. When the carrier orientations of a plaid are separated by less than 90° coherence is perceived whereas transparency regularly occurs with larger orientation separations (Alais et al., 1998; Kim & Wilson, 1993).

Figure 5: Motion coherence thresholds (75%) for the 2 c/° and 6 c/° stimuli used in Experiment 4. The error bars represent ± 1 standard error.
6.5.5 Experiment 5: Low-level factors determine motion integration

Our initial experiments were based on the premise that the percepts associated with the occluded-aperture reflect the ability for the low-level motion system to support either transparency or integration. This hypothesis follows from the fact that many experimental manipulations that change the percept of occluded-aperture stimuli also similarly affect the perception of motion transparency for conventional motion stimuli (Lorenceau & Alais, 2001; Takeuchi, 1998). However, direct comparison with studies using conventional motion stimuli is difficult because of differences in stimulus strength and spatial frequency which greatly affect integration (Amano, Edwards, Badcock, & Nishida, 2009b; Dickinson, Broderick, & Badcock, 2009; Heeger, Simoncelli, & Movshon, 1996; Tang et al., 2013). Our stimulus allows us to overcome this limitation because the same motion information can be maintained while eliminating the second-order form information. Taking advantage of this, the present experiment investigated whether manipulations (peripheral presentation, low contrast, higher spatial frequency) that cause increased integration for the occluded-aperture stimuli have the same effect for stimuli without extended contour information.

To do this, the stimulus was modified to remove the explicit form information while retaining the same motion information (e.g. same number of Gabors, directions). The Gabors were made to have the same orientation content as the four-sided (diamond) stimulus from the previous experiments but were randomly distributed (but made to not overlap with other Gabors) and presented over the same sized area (Movie 7). For example, the Gabors had one of two orientations (separated by 90° and in equal proportions), while the drift rates were still consistent with a globally-defined IOC circular translational direction. Depending on the parameters, the stimulus could give a clear sense of either transparency of integration and, therefore, allowed us to control
low-level factors that influence motion sensitivity by using the same number of Gabor over the same area as the occluded-aperture stimuli (Dickinson et al., 2009; Tang et al., 2013).

Movie 7: The peripheral presentation example from Experiment 5. The stimulus contains randomly-distributed Gabors with the orientations being consistent with the fours sides of a diamond, i.e. there are two directions of motion consistent with global circular motion. The same parameters are used in each presentation instance. Motion transparency will be perceived when fixating on the center of the display. However, if you view the stimulus in the periphery then the stimulus will likely appear to globally integrate.

We used this stimulus to explore a number of low-level factors have been shown to consistently determine whether the occluded-aperture stimulus is seen to be integrated or segmented. We measured global motion coherence thresholds for the randomly-distributed stimulus, with two orthogonal motion directions, in three conditions. The first condition explored how presentation eccentricity affects motion transparency; a manipulation which also changes the percept of the occluded-aperture stimulus from segmented to integrated (Lorenceau and Alais, 2001). Lorenceau and colleagues have argued that their results show that form influences motion processing at a relatively early cortical processing stage. However, a previous study has also shown the perception of transparency for a pseudo-plaid stimulus similarly changes with
peripheral presentation, possibly suggesting a non form-based explanation for the effect (Takeuchi, 1998).

We measured motion integration for the randomly-distributed stimulus at various presentation eccentricities to investigate whether the previous result was due to decreased motion transparency perception. To do this, the stimuli were presented at six distances (0°, 1°, 2.35°, 6.08°, 9.79°, 13.5°) from the fixation point. Movie 7 shows that the stimuli were perceived to be segmented when viewed centrally, but these same stimuli are perceived to be globally integrated when viewed peripherally. The measured coherence thresholds showed the same pattern of results as the demonstrations (Figure 6A). Thresholds were high (>80%) when observers perceived transparency and decreasing when observers could see the global motion direction (and thus perceived integration). A one-way repeated-measures ANOVA confirmed thresholds decreased with increasing eccentricity, \( F(1, 5) = 4.07, p = .03, \eta_p^2 = .67 \). Motion integration (with corresponding decrease in transparency), therefore, increases with peripheral presentation.

![Figure 6](image_url)

**Figure 6:** Motion coherence thresholds (75%) measuring the effect of low-level stimulus properties in Experiment 5. The randomly-distributed Gabor stimulus, representing four sides of a diamond (i.e. two motion directions) was used. The error bars represent ± 1 standard error. The stimuli were presented centrally at 100% contrast with a spatial frequency of 2 c/° unless otherwise noted. (a) Changing the location of stimulus presentation. (b) The contrast of the stimulus was varied between 5 and 100% in logarithmically-spaced steps. (c) The spatial frequency of the stimulus was varied between 2 and 10 c/°.
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The next manipulation sought to explain why integration increases for the occluded-aperture stimulus with decreasing contrast levels (Lorenceau & Alais, 2001; Lorenceau & Shiffrar, 1992; Shiffrar & Lorenceau, 1996). Lorenceau and colleagues argued that decreasing the contrast reduces the salience of intrinsically-attributed terminators which would convert 1D to 2D motion signals and thereby stop global integration. However, motion integration also increases with decreasing contrast for pseudo-plaid stimuli which would not generate line terminators (Takeuchi, 1998), providing an alternative explanation for this change in percept.

The next condition examined whether decreasing motion transparency at lower contrasts explains the results from Lorenceau and colleagues. Movie 8 shows the contrast of the randomly-distributed stimuli decreasing in six logarithmically-spaced steps from 100% to 5% (if viewed on a gamma corrected monitor). Similar to the effect of reducing contrast on the occluded-aperture stimulus (Lorenceau & Alais, 2001; Lorenceau & Shiffrar, 1992; Shiffrar & Lorenceau, 1996), the randomly-distributed Gabors appear transparent at high-contrast levels but globally integrated at lower-contrast levels.
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Movie 8: The contrast manipulation from Experiment 5. The stimulus changes from being perceived as the two planes of translation motion to one single, globally-integrated motion as the contrast decreases in each instance. On a gamma-corrected monitor the stimulus contrast will change in logarithmically-spaced steps.

Consistent with the demonstrations, coherence thresholds decreased with decreasing contrast (Figure 6B). An ANOVA confirmed that thresholds decreased when the contrast of the stimulus was decreased, $F(1, 4) = 8.51, p = .006, \eta_p^2 = .81$. The current result suggests that decreasing the contrast increases integration for the occluded-aperture stimulus because of decreased motion transparency since there are no clear terminators, again replicating Takeuchi (1998).

The next manipulation examined our consistent finding that higher-spatial frequency stimuli (6 c/°) are integrated in conditions where lower spatial frequency stimuli (2 c/°) are segmented. To our knowledge, no studies have determined how motion transparency is affected by the overall spatial frequency. Note that Kim and Wilson (1993, 1996) examined the effects of transparency across components with different spatial frequencies, but did not simultaneously vary the spatial frequency of both components together.

Movie 9 shows the effect of varying the spatial frequency between 2 and 10 c/°
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in logarithmically-spaced steps on motion transparency. Transparency is evident at lower spatial frequencies, whereas integration dominates at higher spatial frequencies. The spatial frequency of the stimulus was varied in the final condition, with integration increases with increasing spatial frequency (Figure 6C). An ANOVA again confirmed that thresholds decreased with increasing spatial frequency, $F(1, 5) = 3.40, p = .047$, $\eta_p^2 = .63$. Again, this suggests that our previous findings where higher-spatial frequency stimuli are integrated is because of decreased motion transparency.

**Movie 9:** The spatial frequency manipulation from Experiment 5. The spatial frequency of the stimulus changes from 2 to 10 c/° in six logarithmically-spaced steps. Motion integration increases with spatial frequency.

The linearly increasing orientation bandwidths with increasing spatial frequency (Anderson & Burr, 1985; De Valois et al., 1982) could explain this result. At low spatial frequencies, motion transparency only occurs when motion directions are separated by more than 45°, otherwise integration occurs (Alais et al., 1998; Kim & Wilson, 1993). This separation may be influenced by the orientation bandwidth, which determines whether two motion directions generate independent or overlapping neural population responses. The separation between directions necessary for transparency would, likely increase as the orientation bandwidth increases with spatial frequency.
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Taken together these results suggest that increasing noise by degrading the stimulus representation (by lowering contrast, presenting the stimuli in the periphery, reducing direction separation, or increasing the spatial frequency) benefits motion integration while simultaneously degrading motion transparency. These results can be generalized to the occluded-aperture stimulus to show that segmentation is perceived in conditions of low noise that allow for simultaneous perception of more than one motion direction (transparency). Whereas conditions of high noise cannot support multiple motion directions and the perceived motion direction is instead given by the vector average or IOC solution of the components. Overall, these results strongly suggest that motion-pooling mechanisms mainly determine the percepts of the occluded-aperture stimulus rather than the purported high-level or form-based explanations (Lorenceau & Alais, 2001; Lorenceau & Shiffrar, 1992; Shiffrar & Lorenceau, 1996).

6.5.6 Experiment 6: Effect of shape type (number of sides)

So far, we have shown that the change in percepts of the occluded-aperture stimuli can be explained by the motion representation; without any reference to form information. However, one of the most striking demonstrations with occluded-aperture stimuli cannot readily be explained by the same low-level description. This demonstration shows that integration only occurs when the shapes form closed, but not open, contours (Lorenceau and Alais, 2001). Lorenceau and Alais (2001) suggested that these results imply that form information acts to determine which motion signals are pooled and which are segmented, ‘vetoing’ integration when there is are open contours. This original study did not, however, determine whether the closed contour conversely enhances motion integration. Furthermore, their theory was recently challenged by a demonstration showing shapes, without any closed contour information, that are translating behind apertures can be integrated (Kane et al., 2011; Kane et al., 2009)
suggesting that a closed contour is not needed for motion integration.

Our stimulus is well suited to address the apparent conflict between these results as it can be readily modified to make both open and closed contours. Furthermore, the stimulus can be modified to remove the form information while retaining the same low-level motion information. A manipulation that would determine whether closed contours conversely enhances integration. In this experiment, two new stimulus configurations were compared to the previous results for closed contours shapes. The stimuli in the ‘open’ condition were identical to those used in Experiment 1, except that angle of each side of the polygon was rotated by $90^\circ$ (Movie 10A). The randomly-distributed Gabors from Experiment 5 were employed to keep the low-level information identical between conditions while removing the second-order shape information (Movie 10B). The stimuli were made to have the same orientation content as the matching number of side conditions, thus maintaining the same direction separations. For examples, the Gabors were evenly distributed between one of three orientations in the three-sided condition, with the drift rates consistent with the 2D global motion direction. The stimuli in this condition will show how integration thresholds for the motion information contained in the occluded stimuli are affected by the extended contour information. The spatial frequency of the Gabors was $2 \text{c/}^\circ$ in both shape-type conditions as the previous experiments have shown an effect of number of sides at this spatial frequency.
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Movie 10: Examples of the stimuli used to determine the effect of the type of shape on motion pooling in Experiment 6. Left panel: the open condition with between three and eight sides. The stimuli are identical to the closed contour condition in Movie 1 except each side is rotated by 90°. Note the demonstration has been resized to for this presentation but the spatial frequency used for testing was identical to Experiment 1. Right panel: The stimuli used in the random condition. There is the same number of Gabors as the open and closed condition but the overall shape information is removed by randomly distributing the Gabors.

We quantified these effects by measuring the motion coherence thresholds for the open and random stimulus configurations, comparing them to thresholds found for the 2 c/° condition in Experiment 1 (closed shape). Figure 7 shows the motion coherence thresholds for the three types of shapes with different numbers of sides. As in previous studies (Lorenceau & Alais, 2001), shapes forming open contours were less effectively integrated than shapes forming closed contours. Thresholds for the randomly-distributed Gabors were relatively unchanged as number of sides increases except when there is four sides where, consistent with Experiment 5, motion transparency was perceived. All other number-of-side conditions for the randomly-distributed stimuli were globally integrated, leading to lower thresholds.
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Figure 7: Motion coherence thresholds (75%) measuring the effect of varying the number of sides for closed, open and random conditions in Experiment 5. All stimuli were presented at 2°. The error bars represent ± 1 standard error.

To confirm these observations, we compared thresholds using a 6 (number of sides) × 3 (shape type) repeated-measures ANOVA. Thresholds significantly changed with an increasing number of sides, $F(5, 10) = 10.27, p = .001, \eta_p^2 = .24$, and were different between the shape types, $F(2, 4) = 7.37, p = .046, \eta_p^2 = .27$, and there was a significant interaction between number of sides and shape types, $F(10, 20) = 5.33, p = \text{.0007}, \eta_p^2 = .23$. These results may suggest that the overall shape information plays an important role in determining which motion signals are integrated (Lorenceau & Alais, 2001). Open shapes were rarely perceived to be globally integrated, even when there were a large number of sides. When the closed shapes integrated with more than four sides, thresholds were similar (or even slightly higher) than in the randomly-distributed condition, suggesting that the form information does not conversely increase sensitivity to global motion.

The results also suggest that the global form information can only veto, not enhance, global motion pooling, as thresholds were similar for random and closed contour conditions. This result reconciles the apparent conflict between previous studies.
Integration occurred in the later studies (Kane et al., 2011; Kane et al., 2009) because the shapes did not form an explicit open contour (they were similar to our randomly-distributed condition), where integration is vetoed. The impact of closure on integration is similar in static shapes as observers can be less sensitive for shapes forming open, compared to closed, contours which was especially pronounced when the boundary was incomplete (Tversky, Geisler, & Perry, 2004 but see Dickinson, McGinty, Webster and Badcock (2013) for radial frequency patterns).

6.5.7 Experiment 7: Effect of shape type (orientation range)

Experiment 4 found that allowing the orientation range of the three-sided stimuli to vary over 45° causes motion integration performance to greatly improve compared to when all Gabors were aligned parallel to the contour. In this experiment, we explored whether a very large orientation (1D motion direction) range would allow shapes forming open contours to be integrated. To do this, the orientation range (in the same manner as Experiment 4) of three-sided version of the open and randomly-distributed shape types was varied (Movie 11). The movie shows that there is some sense of global motion when there is a large amount of orientation range for the open shape type. The randomly-distributed Gabors with three sides represented show motion integration regardless of the orientation range.
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Movie 11: Examples of the stimuli used in Experiment 7. The range of orientation is increased in each presentation with the orientations of the Gabors varying over 180° in the final presentation. Left panel: The stimuli for the open shape condition are the same as the three-sided condition (the stellated triangle) used in Experiment 5. Note the demonstration has been resized to for this presentation but the spatial frequency used for testing was identical to Experiment 1. Right panel: The stimuli from the randomly-distributed shape type condition. The stimuli are the same as the three-sided condition for the random shape in Experiment 5.

Motion coherence thresholds were measured when the orientation range was varied for the open and randomly-distributed Gabors. These were compared to the results for the closed shapes from Experiment 4 (Figure 8). These show that the orientation range required for the open shape to become strongly integrated is significantly higher than for the closed shape. Nevertheless, the shapes forming open contours are more effectively integrated when the orientation range is large, suggesting the overall importance of orientation range and direction separation for these stimuli. Thresholds for the randomly-distributed stimuli appear relatively unchanged regardless of the orientation range of the stimulus. A 6 (orientation range) × 3 (shape type) repeated-measures ANOVA confirmed this pattern of results. Thresholds significantly decreased when the orientation range increased, $F(5, 10) = 15.42, p = .0002, \eta^2_p = .16$. Thresholds were also significantly different between the three shape types, $F(2, 4) =$
34.32, $p = .003$, $\eta_p^2 = .55$, which significantly interacted with orientation range, $F(10, 20) = 3.20, p = .01$, $\eta_p^2 = .12$. These results suggest that any type of contour will become integrated when the orientation range is very large.

Figure 8: Motion coherence thresholds (75%) measuring the effect of varying the orientation range for closed, open and random conditions in Experiment 7. All stimuli were presented at 2 c/°. The error bars represent ± 1 standard error.

6.6 Conclusions

The present work examined the role of shape information in the recovery of global motion integration using the extensively employed occluded-aperture stimulus which has been argued to show how form information influences this process (Lorenceau & Alais, 2001; Lorenceau & Shiffrar, 1992; McDermott & Adelson, 2004; McDermott et al., 2001). The study had two main aims; firstly to investigate whether low-level motion information causes the percepts for the occluded-aperture stimulus to change rather than the purported high-level form-motion interaction. The second aim was to resolve a conflict in the literature about the importance of closed contour information in motion pooling. We found that the percepts for occluded-aperture stimuli result from an interplay between motion integration and segmentation, similarly to
conventional motion stimuli. This interplay is mainly governed by low-level motion mechanisms that are sensitive to the directional separation, spatial frequency and contrast of the stimuli. The overall shape information only affects global motion sensitivity when the shape explicitly forms an open contour, where the ability to integrate is reduced compared to randomly-distributed and closed-contour stimuli.

The initial manipulations sought to determine whether the previous studies’ consistent use of four-sided stimuli (Lorenceau & Alais, 2001; Lorenceau & Lalanne, 2008; Maruya & Nishida, 2010; McDermott & Adelson, 2004; McDermott et al., 2001; Shiffrar & Lorenceau, 1996) limited the generalizability of the conclusion. This configuration leads to motion directions separated by $90^\circ$, the mid-point of transparency and integration for conventional motion stimuli (Alais et al., 1998; Kim & Wilson, 1993). When varying the directional separation by changing the number of sides, it was found that motion integration was poor when the stimulus had three or four sides but was greatly improved when it had more than four sides (Experiments 1-2). A consistent effect of spatial frequency was also found, with integration performance increasing with spatial frequency regardless of the number of sides.

It was then found that motion integration occurs when there are more sides because of the number of orientations (co-incident with 1D directions) represented (Experiment 3-4). Observers could readily discern the global direction when we modified a three-sided stimulus to have two orientations represented in each side, showing that orientation information (coinciding with directional separation) limits motion integration. We then built upon this finding showing that the motion integration occurs when the orientations of the Gabors making up each side were allowed to vary by over $45^\circ$. Experiment 5 confirmed that the percept for the occluded-aperture stimulus generally occurs because the ability to support one or two motion directions. When we
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equated motion stimulus strength but removed form information, the same
manipulations (low contrast, peripheral presentation and increased spatial frequency)
reduced motion transparency (increasing integration) that increases integration for the
occluded aperture stimulus. Our results can be explained in terms of the representation
of low-level motion information and mechanism tuning. If there is little stimulus noise
then each side of the shape can cause a unique motion direction to be represented in the
population response (allowing for motion transparency), but the sides will produce
overlapping responses when there is high stimulus noise, leading to integration.

The next line of enquiry examined a previously-used manipulation of the
occluded-aperture stimulus that cannot be easily explained by a low-level motion
explanation (Experiment 6-7). Lorenceau and Alais (2001) found that shapes forming
closed, but not open, contours integrated, but later studies (Kane et al., 2009, 2011),
using stimuli presented behind many apertures found that open shapes could be globally
integrated. The similar thresholds between these conditions suggest that the presence of
a closed contour does not conversely enhance motion integration sensitivity compared
to when there is no contour. Under our proposed framework for
integration/segmentation for this stimuli, the result suggests that presence of an open
contour acts as a segmentation cue leading to transparency. This is, at least partially,
consistent with findings that items that are perceptually grouped are more readily
segmented into a single perceived motion direction (McOwan & Johnston, 1996).

Throughout the manuscript, we have examined whether segmentation can be
considered an aspect of motion transparency where observers can report two (or in some
cases, three) simultaneous motion directions (Greenwood and Edwards, 2006, 2009).
Reducing the contrast, increasing the spatial frequency, peripheral presentation
(Lorenceau and Shiffrar, 1992; Lorenceau and Alais, 2001; Shiffrar and Lorenceau,
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1996), higher spatial frequency and reducing the directional separation increase integration for the occluded-aperture stimulus and conventional motion stimulus without any extended form information. We suggest that these results indicate that transparency only occurs when each motion direction produces a distinct population response and is, thus, limited by stimulus and mechanism representation (Braddick, Wishart, & Curran, 2002; Greenwood & Edwards, 2006; Qian & Andersen, 1994; Takeuchi, 1998). Note, however, there is some evidence that integration may differ depending on the motion type (e.g. translation and rotation) which could also affect transparency (Lee & Lu, 2010).

However, it is possible these results could be considered within a proposed Bayesian framework of motion integration (Weiss, Simoncelli, & Adelson, 2002). This study showed that motion integration changes (from IOC to VA) depending on stimulus contrast, which modulated stimulus certainty. Our stimulus manipulations (e.g. spatial frequency, directions) could similarly be considered to affect certainty. For example, there is less certainty about individual directions represented when the separation between directions decreases because there will likely to be greater overlap in the population response. This could lead to motion transparency occurring when observers are highly certain of individual directions but increased integration across the directions with more certainty.

6.6.1 Conclusion

Overall, we have provided strong evidence that the occluded-aperture stimulus is more closely related to standard global motion displays (i.e. plaids, global Gabor) than previously thought. Our results suggest that the percept mainly changes from motion segmentation to integration depending on the representation of each motion representation. If multiple motion directions can be extracted then shape is perceived to
segment into independently translating sides, but if multiple directions cannot be extracted then signals are integrated resulting in perception of veridical global motion direction.

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6.8 References


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7 General Discussion

The central aim of this thesis was to examine the role of form information in motion processing. The dominant theories of motion perception generally overlook this topic as these are based on extensive neurophysiological evidence showing that form and motion information is processed in relatively independent neural pathways (Braddick, O'Brien, Wattam-Bell, Atkinson, & Turner, 2000; Livingstone & Hubel, 1987; Mishkin, Ungerleider, & Macko, 1983). There is also a large amount of psychophysical research showing that form is independent of motion and motion independent of form. For example, Exner (1888) showed that observers can resolve motion between two lights that are so close together that they appear as a single object, suggesting that object perception is not always necessary for the perception of motion. Anstis (1980) built upon these results by showing that apparent motion follows the luminance distribution not form matches, indicating global form information is not a critical feature for motion perception. Furthermore, observers can identify shape information presented for 40 ms, a presentation time which precludes eye movements from generating coherent motion signals (VanRullen & Thorpe, 2001). Conversely, a randomly-distributed field of moving dots without any global, second-order form
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information can give the vivid impression of coherent motion (Newsome & Pare, 1988; Williams & Sekuler, 1984).

More recently, however, there is a growing literature showing that form information can sometimes directly affect relatively early stages of motion processing. For example, a small number of moving dots can give the vivid impression of a moving human or animal (Johansson, 1973, 1976) or segment a shape from a background if moving in a common manner (Landy, Dosher, Sperling and Perkins, 1991; Sekuler, 1990; Ullman, 1979). Sequentially presenting Glass patterns, containing undirected motion energy, causes the perception of motion along the path implied by the global pattern orientation (Badcock & Dickinson, 2009; Ross, Badcock, & Hayes, 2000). Such examples of perception of illusory motion strongly suggest that form information can channel undirected motion signals by somehow influencing the motion processing system.

The notion that form information can affect motion integration has also been supported by studies showing that providing a form cue in a standard global motion stimulus changes the manner which the motion signals are integrated (Amano, Edwards, Badcock, & Nishida, 2009; Edwards, Cassanello, Badcock, & Nishida, 2013). The perceived path of an apparent motion stimulus can also follow the shape of a surrounding form cue, overriding the path implied by normal nearest-neighbor matching (Kim, Feldman, & Singh, 2011). Finally, extensive evidence shows that global form information can determine whether motion signals cause integrated or segmented precepts suggesting a form-motion interaction at the stage of global pooling (Lorenceau & Alais, 2001; Lorenceau & Lalanne, 2008; Lorenceau & Shiffrar, 1992; McDermott & Adelson, 2004; McDermott, Weiss, & Adelson, 2001; Shiffrar & Lorenceau, 1996).

This thesis examined how form information affects three key tasks of the motion
system: detection, direction processing and integration. Chapter 2 examined a novel form-motion interaction where a form signal causes the perception of motion. It was shown that this unique motion information enters the motion system by, at least, the stage of global integration. Chapters 3-5 examined how orientation information influences motion direction processing. Chapter 3 tested the influential form-motion model of motion streaks. Motion streaks are orientation signals proposed to be caused by the extended integration time of visually-selective neurons in V1, which cause fast moving objects to leave the neural equivalent of a form signal along the motion axis (Badcock & Dickinson, 2009; Geisler, 1999; Geisler, Albrecht, Crane, & Stern, 2001). The original model (Geisler, 1999) argued that motion streaks allow motion information to be processed with the fidelity of form because orientation and motion are multiplicatively combined in V1. The results presented in Chapter 3, instead, suggested that the orientation information from the streak enters the motion system at a later stage, most likely during global motion integration. A new model of motion streaks was developed to account for these results and was tested in Chapters 4-5. Chapter 6 built upon the previous chapters to determine how the form information that enters the motion system affects motion integration, one of the key challenges of the motion system.

7.1 Summary of results

This section contains a more detailed description of the experimental results presented in the thesis and the implications.

7.1.1 Form signals alone can generate a motion percept

The results presented in Chapter 2 showed that motion information generated by form changes most likely enter the motion system by the stage of global motion integration. Transformational apparent motion (TAM) is produced when an
instantaneous form change gives the impression of motion in the direction that explains the shape change (Tse, 2006; Tse & Caplovitz, 2006; Tse, Cavanagh, & Nakayama, 1998; Tse & Logothetis, 2002). TAM is unique because, in some stimulus configurations, low-level motion energy models do not predict the perceived motion direction. Because of this property, it has been suggested that TAM arises from a high-level form-motion pathway, separate from the low-level motion energy-based mechanisms (Baloch & Grossberg, 1997; Francis & Grossberg, 1996; Tse et al., 1998; Tse & Logothetis, 2002). However, the mechanism that processes TAM has yet to be fully elucidated, mainly because the stimulus used in many studies can be explained by low-level motion detection (Chica, Charras, & Lupiáñez, 2008; Downing & Treisman, 1997; Hikosaka, Miyashita, & Shimojo, 1993a, 1993b; Tse, 2006).

In the experiments outlined in Chapter 2, we sought to determine where the TAM signal enters the motion system. This was done by examining whether multiple, simultaneously-presented TAM signals can generate a unified global motion percept. In some circumstances, these signals produced a global percept of TAM, but were often relatively easily overridden by low-level motion energy cues. Global motion was perceived in the opposite direction to single element TAM when the motion energy cue was strong, whereas global motion was perceived in the TAM direction if the motion energy cue was reduced. These results suggest that TAM enters the motion system by, at least, the stage of global motion pooling, most likely V5 or MST, but the TAM input is relatively weak compared to motion energy. This is an important contribution as most existing models of visual perception argue that form and motion information are separately processed. These results, instead, suggest that form information can enter the motion system by the stage of global motion integration.
7.1.2 Orientation information enters the motion system by the stage of global integration

The experiments presented in Chapters 3-5 built upon the results from Chapter 2 showing how the form information that enters the motion system influences motion direction processing. The experiments described in Chapter 3 examined Geisler’s (1999) model of motion streaks. Geisler argued that the extended integration time of neurons in early visual cortex cause moving objects to create form cues along the axis of motion. He presented a model arguing this orientation information is multiplicatively combined in V1 with the ambiguous motion direction signal. This type of combination causes the motion signal to inherit the directional precision of form information. A number of studies have shown that fast motion appears to create oriented form information in V1 (Apthorp & Alais, 2009; Apthorp, Cass, & Alais, 2010; Apthorp, Cass, & Alais, 2011; Apthorp et al., 2013; Apthorp, Wenderoth, & Alais, 2009; Geisler, 1999; Geisler et al., 2001). However, no study had provided a comprehensive test of the Geisler’s prediction that streak information allows motion signals to be processed with the fidelity of form information.

Geisler’s model was tested using an aftereffect where adapting to an oriented grating causes the perceived direction of subsequently-presented motion to appear repelled away from the adapted orientation. It was found that a much broader range of orientations caused aftereffects than predicted by the original model. In fact, the orientation dependence was more than double that of static form-test stimuli and was, instead, similar to a motion direction aftereffect measured using stimuli which would not cause motion streaks (Schrater & Simoncelli, 1998). This result was built upon by showing that perceived motion direction could be either be attracted or repelled from the adapting orientation depending on the spatial frequency of the adaptor. The
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orientation and spatial frequency dependency of the aftereffect are both consistent with orientation affecting the stage of global motion integration. It was then shown that increasing the excitability of V1 reduces the magnitude of the aftereffect, suggesting that the orientation information from the streak is gathered at this area. A new model for motion streaks was accordingly proposed which argues that orientation-selective neurons directly modulate the gain of motion-selective neurons at the stage of global motion pooling. The model successfully accounts for the extant results.

Experiments in Chapter 4 provided a strong test of a prediction from the proposed form-motion model outlined in Chapter 3 where orientation information directly influences the gain of motion-selective neurons at the stage of motion integration. A prediction from this model was tested in Chapter 4 by showing that adaptation to a static grating changes the perceived direction of a subsequently-presented global plaid array. Because of the specific stimulus construction, the perceived change in direction could not be due to adaptation affecting local motion processing and, instead, most likely reflects changes at the stage of global motion integration. Furthermore, the proposed model accurately predicted the measured orientation dependence of this aftereffect. We also confirmed that adaptation to static form can cause either attractive or repulsive aftereffects depending on the spatial frequency relationship between the adapter and test stimuli. The same adaptation procedure leading to either attractive or repulsive aftereffects was then shown to affect global motion pooling thresholds, again suggesting the sensitivity of global motion neurons was being modulated.

Together, the experiments presented in Chapters 3 and 4 showed that adapting to orientation changes the perceived direction of subsequently-presented motion. The experiments reported in Chapter 5 further expanded these results by showing that the
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shape of a moving object can influence its perceived motion direction. Specifically, form information, simultaneously presented with a motion signal, can change the perceived direction of motion. We presented a new form-motion illusion where the shape of a field of Gabor-like elements was influenced by the envelope orientation. Furthermore, envelope orientation could either attract or repel the perceived motion direction similarly to results in Chapters 3 and 4. The results showing that simultaneously-presented orientation can either attract or repel motion direction allowed us to explain four previously-published illusions that had mainly been attributed to other factors. The model accurately predicted all the illusions suggesting that orientation directly affects motion processing at the stage of global motion integration in a manner predicted by the model.

The finding that orientation information directly modulates motion-sensitive neurons by the stage of global motion integration may be important for understanding motion processing. Traditional motion pooling solutions (i.e. intersections-of-constraints and vector averaging) do not allow for form information to change the derived motion solution in a systematic manner. But, as previously stated, there is now increasing evidence that form can directly affect motion direction. The form-motion model presented in this thesis shows how this form information might enter the motion system and influence processing. Specifically, the connection between orientation and motion-selective neurons in different cortical regions could input into intersection-of-constraints and vector averaging pooling solutions (Adelson & Bergen, 1985; Adelson & Movshon, 1982; Amano et al., 2009). This would potentially allow these solutions to incorporate form information to change their overall outcome. It is likely that form information affects the vector averaging solution. Motion pooling solutions change from intersection-of-constraints to vector averaging when the signals change from 1D to
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2D by introducing plaids (Amano et al., 2009) or by adding form cues to the envelope of Gabors (Edwards et al., 2013).

The proposed form-motion model could also explain a number of other real-world effects. Comics have traditionally used lines originating from characters to signal motion direction (Figure 1). The extended integration time of visually-selective neurons leads to the ‘raw’ neural image of moving objects to appear similarly streaky (Burr, 1980; Geisler, 1999). Thus, the low-level images of moving objects are likely to resemble the comic speed lines.

![Figure 1. A comic showing how motion streaks have been commonly used to represent motion direction in static images. ‘Train’ from xkcd by Randall Munroe from https://xkcd.com/1366/ used under a Creative Commons license.](image)

An interesting outcome of the current work is that the model can explain how artificially streaking a picture, in the manner used by comic artists, may actually cause
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motion to be perceived in the picture. For example, Figure 2 shows a static image of a man jumping, captured using a relatively long aperture time. The image can give the vivid impression of motion constrained along the vertical axis. The proposed form-motion model can explain this as the orientation cue from the streak is increasing the gain of the corresponding motion-sensitive neurons at the stage of global motion integration. Any small motion, say from eye movements, would cause motion energy to be channeled along the orientation axis leading to the impression of motion along the streaked direction. This result provides an interesting counterpoint to the original speed lines from comics because it suggests these lines may actually cause the motion system to activate in the signaled direction. Some evidence for this prediction comes from studies examining implied motion, where a static image gives the impression of movement. One study showed that adaptation to these images causes the motion aftereffect in a subsequently-presented incoherent global dot motion stimulus (Winawer, Hu, Boroditsky, 2008)

Figure 2. Photograph of “Killer Joe Piro” by Richard Avedon. The face appears to move vertically along the streaked direction.
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7.1.3 The role of form in motion pooling and segmentation

Chapters 2 to 5 provided strong evidence that orientation information influences motion processing by the stage of global motion integration. One of the key roles of this stage is to pool multiple motion sources together to yield a unified global percept resulting from one object, while disregarding signals from other objects. If form information is entering the motion system by the stage of global motion integration, it is possible this information is used to determine which signals are integrated and segmented. Form could be useful for this process as shape information could unambiguously indicate which motion signals belong to the same or different objects. The occluded-aperture stimulus has been extensively used to investigate the role of form information in motion integration (Lorenceau & Alais, 2001; Lorenceau & Lalanne, 2008; Lorenceau & Shiffrar, 1992; McDermott & Adelson, 2004; McDermott et al., 2001; Shiffrar & Lorenceau, 1996). One of the main findings from work is that shapes forming open contours (e.g. a cross) are not globally integrated while those that form open contours (e.g. a square) are.

The experiments in Chapter 6 build upon the previous finding that form information enters the motion system by the stage of global motion integration by employing the occluded-aperture stimulus. A novel version of the stimulus was developed where the shape’s contour was constructed from many individual Gabor patches. This had the benefit of controlling for spatial frequency and allowing for the separation of motion and form signals. A series of experiments found that motion was globally integrated when the shapes had more than four sides or presented at higher spatial frequencies. The results suggested the fidelity of low-level motion signals determined whether the shape was perceived to be integrated or segmented. We argue that the shapes appear segmented under conditions where motion transparency is
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possible, whereas integration is perceived under conditions where transparency is not possible.

A previous finding that shapes forming open contours are not globally integrated were then built upon (Lorenceau & Alais, 2001; Lorenceau & Lalanne, 2008). Motion integration for shapes forming open and closed contours was compared to when the stimuli did not contain form information. The results replicated previous findings that shapes forming open contours were less likely to be integrated compared to shapes forming closed contours. However, it was found that motion integration thresholds were similar between closed contour shapes and stimuli without any extended contour information suggesting that shape information does not enhance the recovery of motion, but instead only provides a segmentation cue.

7.2 Future research

The form-motion model that was proposed and tested (Chapters 3-5) in this thesis should be expanded in future work. The model takes the orientation from the adapted, or simultaneously-presented, form information and the motion direction of the stimulus. These values are inputted from the absolute direction and orientation information for each simulation. We chose to represent the model in this algorithmic manner to show a general principal of how form and motion interact that was based on a minimal number of assumptions to allow for greater generalization. However, later work should expand the model so that this information is gathered from stimulus image sequences, by significantly expanding the early stages of the model. Specifically, a field of neurons representing orientation, spatial and temporal frequency could be simulated to mimic V1 response (e.g. Baker and Issa, 2005; Mante and Carandini, 2005). The orientation and motion extracted from this field of neurons could modulate the gain response of the existing motion-selective neurons at the stage of global motion pooling.
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The choices about the specific orientation, spatial and temporal frequency and the degree of representation of each would need to be carefully made as this will alter the low-level inputs.

Another potential avenue for future research comes from the proposed form-motion model which was directly based on the behavioral psychophysical results. These results were argued to show that form information enters the motion system by, at least, the stage of global motion integration with a mechanism provided showing how these interactions could occur. Neurophysiological measurements, using electrophysiology or functional imaging, are needed to determine whether orientation modulates the gain of motion-sensitive neurons at the stage of global motion integration, most likely V5 or MST, in the specified manner. Showing that orientation modulates the gain of motion-selective neurons would support the current conclusions with a different methodology and determine the exact neural locus of the interaction.

7.3 Conclusions

The research presented in this thesis adds to the existing literature on visual processing. The main finding was that form information directly enters the motion system by, at least, the stage of global motion integration. A new form-motion model was developed showing that orientation can directly influence motion processing and the manner in which this interaction could occur. Furthermore, we have shown that the form information influences motion integration. Results from Chapter 2 established that form information can generate a response at this stage. Experiments in Chapters 3-5 built upon this result to show the manner in which form information influences motion processing. A new model of form-motion interactions was developed and tested showing that motion direction processing is modulated along the dominant orientation axis of a shape. This modulation can be either inhibitory or excitatory depending on the
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spatial frequency relationship between the form and motion stimuli. Chapter 6 showed how global form information influences global motion integration, as the previous chapters had shown that form information enters the motion system by this stage.
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