

Role of form information in motion pooling and segmentation

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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

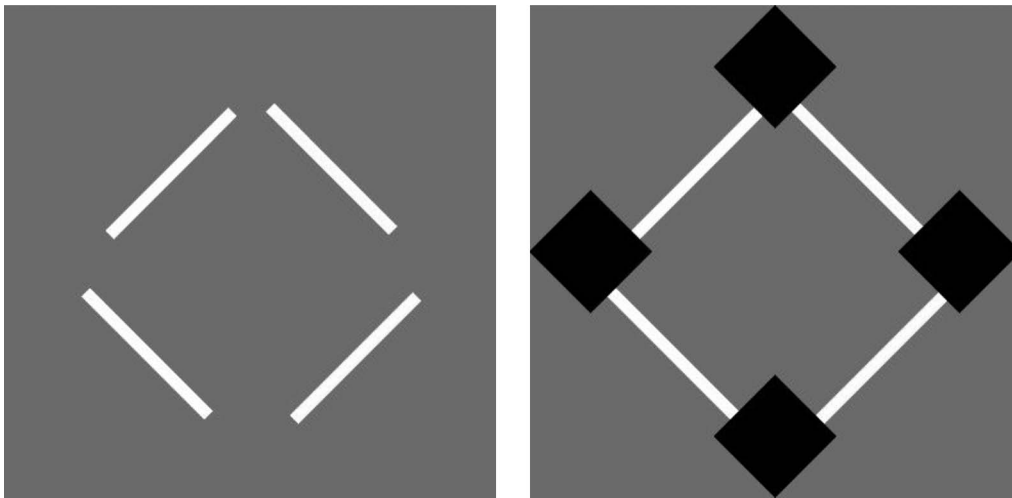
integration is perceived with only a small overall influence of form.

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

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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 anticlockwise direction.

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 toward 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.

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 employed 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), 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.

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, 2009; Kane, Bex, & Dakin, 2011; 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.

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

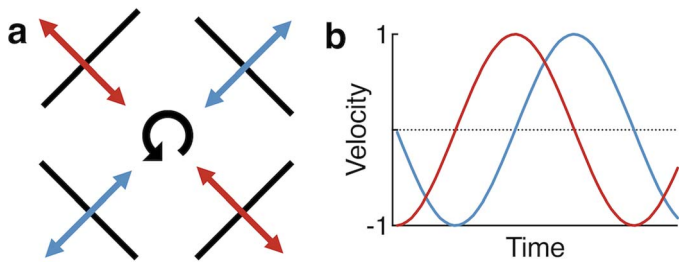


Figure 1. A schematic example of a diamond (four-sided) version of the occluded aperture stimuli (a) and the associated speed of each contour which are subject to the aperture problem (b). Panel b shows the relative velocities of the contours needed to produce circular translational motion. The lines 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.

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 to 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 (Lorenceanu & Alais, 2001; Shiffrar & Lorenceanu, 1996), the change in percept for the occluded-aperture stimulus could possibly 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 previously, with the population response more likely to cause overlap when the directional separation is decreased. If the change in percept for the occluded-aperture stimulus is governed

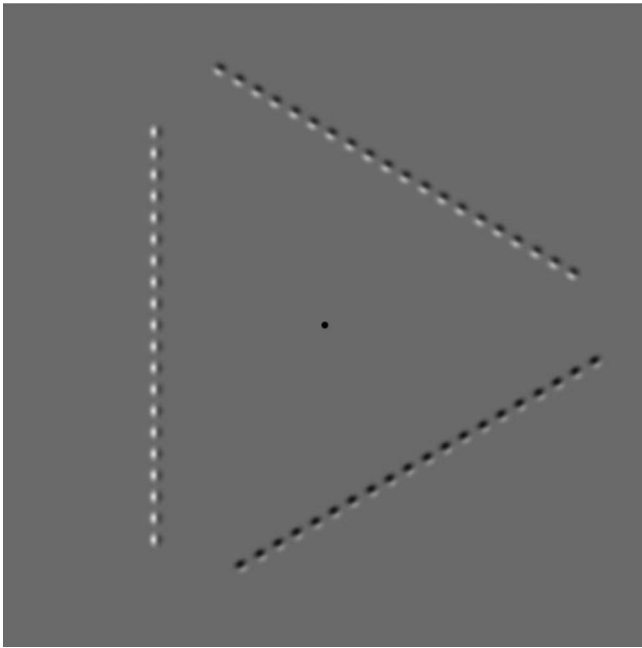
by the low-level motion representation, then decreasing the direction separation should increase motion integration. This could be accomplished by increasing the number of sides, while retaining the closed contour information.

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.

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; Lorenceanu & Alais, 2001; Shiffrar & Lorenceanu, 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 (Lorenceanu & Alais, 2001). This finding has been 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., 2009; Kane et al., 2011). 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.



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 $2\text{ c}/^\circ$ condition in Experiment 1.

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 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.

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 stimu-

lus. 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., 2009; Kane et al., 2011; Lorenceau & Alais, 2001). To address this uncertainty, motion integration for shapes, forming closed or open contours, was compared to stimuli without extended overall form information.

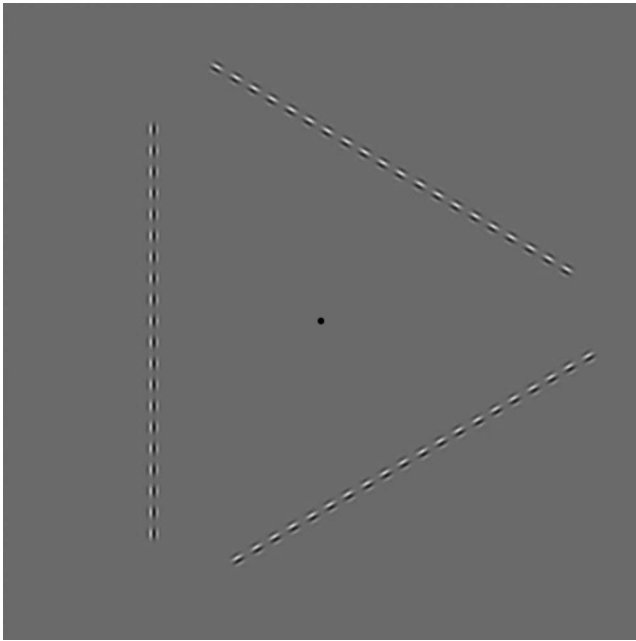
General methods

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.

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 (Nvidia, Santa Clara, CA) using PsychToolbox 3 (Brainard, 1997; Pelli, 1997). The stimuli were displayed on a Sony Trinitron G520 monitor (Sony, Tokyo, Japan) with a 60 Hz refresh rate and a 1280×1024 pixel resolution. A Cambridge Research Systems Bits# system (Cambridge Research Systems, Kent, UK) 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 $32^\circ \times 25.75^\circ$ and thus each pixel had a subtense of 1.5×1.5 feet. The luminance response of the monitor was gamma-corrected using a ColorCAL II photometer (Cambridge Research Systems) and custom-written software. The background of the monitor was set at mid-gray with a luminance of $87.5\text{ cd}/\text{m}^2$, and the maximum white luminance was set at $175\text{ cd}/\text{m}^2$.



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.

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 Gabors 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 Gabors 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 Gabors near the corners and, thus, each side was always a straight line. Unless noted, the Gabors had an envelope standard deviation of 0.06° and were presented at 100% contrast. The number of Gabors on each side of the shape was varied so there were always 60 Gabors 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.

Procedure

Each trial began with a stationary version of a stimulus, surrounding a centrally-presented fixation dot. After 400 ms, the carriers of the Gabors 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 anticlockwise. Analogous 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 pseudorandomized order within each block. Observers completed three blocks of trials for each stimulus condition, with the threshold taken as the mean of the blocks.

Results and discussion

Experiment 1: Varying number of sides

To our knowledge, all previous studies 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 conditions. We simultaneously examined whether spatial frequency affects integration. Movies 2 and 3 show examples of the stimuli used. As can be seen

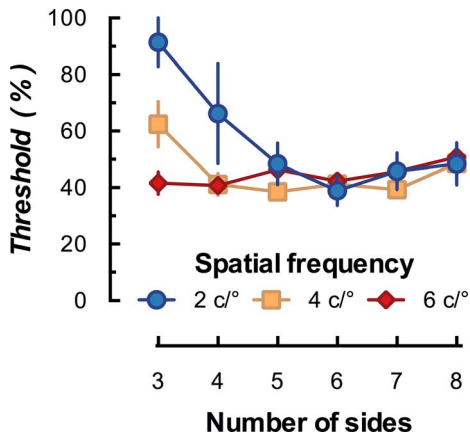
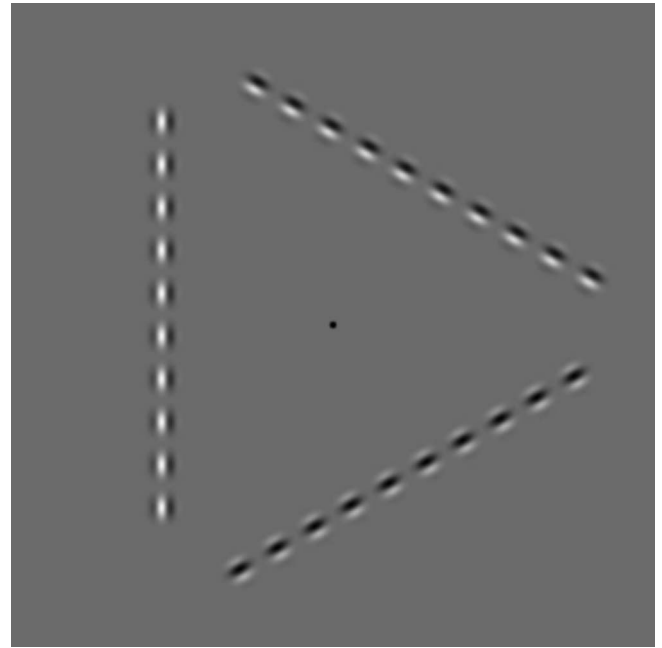


Figure 2. Motion coherence thresholds (75%) for detecting directions of global motion in Experiment 1. The number of sides of the polygon was varied and the spatial frequency of the Gabors making up the contour boundary. The error bars represent ± 1 standard error.

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).

The coherence thresholds for determining whether the shape was rotating in a clockwise or anticlockwise 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 ($< 50\%$).

These thresholds were subjected to a 6 (number of sides) \times 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, $F(5, 10) = 5.59$, $p = 0.01$, $\eta_p^2 = 0.26$, and a marginal main effect of spatial frequency, $F(2, 4) = 5.04$, $p = 0.08$, $\eta_p^2 = 0.12$. Critically, there was also a significant interaction between number of sides and spatial frequency, $F(10, 20) = 3.05$, $p = 0.02$, $\eta_p^2 = 0.28$, 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 $ps < 0.05$),



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/°.

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 $ps > 0.05$). 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.

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 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.

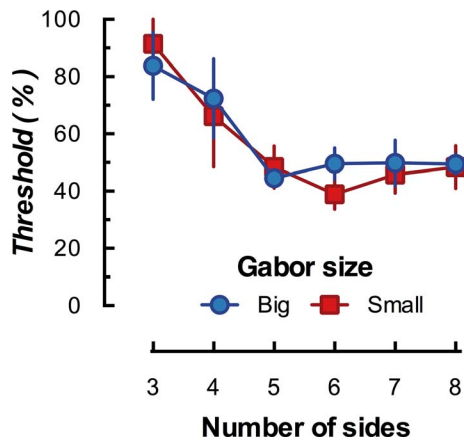


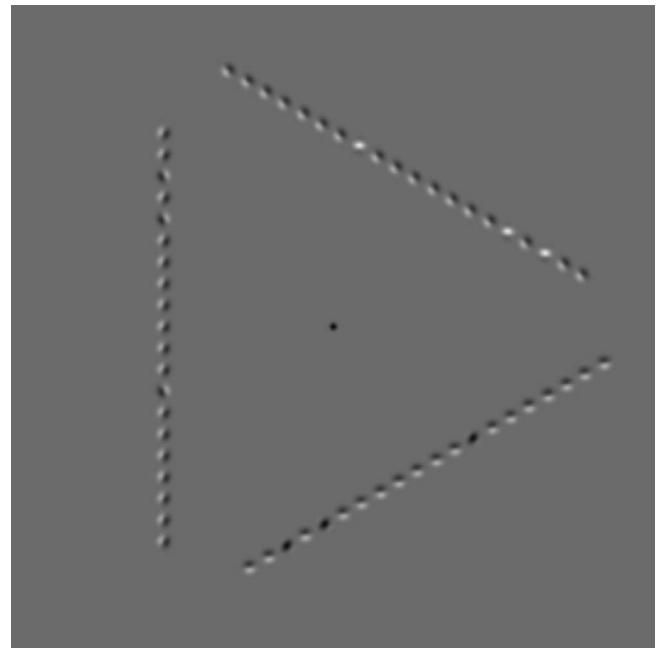
Figure 3. Motion coherence thresholds (75%) for the control condition in Experiment 2. The Gabors had standard deviation of 0.1276° and a spatial frequency of $2\text{ c}/^\circ$. The error bars represent ± 1 standard error.

The motion coherence thresholds for these stimuli were compared to the results to the $2\text{ c}/^\circ$ 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) $\times 2$ (Gabor size) repeated-measures ANOVA supported this observation with thresholds not significantly differing for the two patch sizes, $F(1, 2) = 0.03$, $p = 0.62$, $\eta_p^2 = 0.002$. Thresholds significantly decreased with increasing number of sides, $F(5, 10) = 3.36$, $p = 0.049$, $\eta_p^2 = 0.57$, and there was no significant interaction between factors, $F(5, 10) = 2.42$, $p = 0.11$, $\eta_p^2 = 0.02$. 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.

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).

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

So far, we have found that the occluded-aperture stimulus is only integrated when presented at lower



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.

spatial frequencies, 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

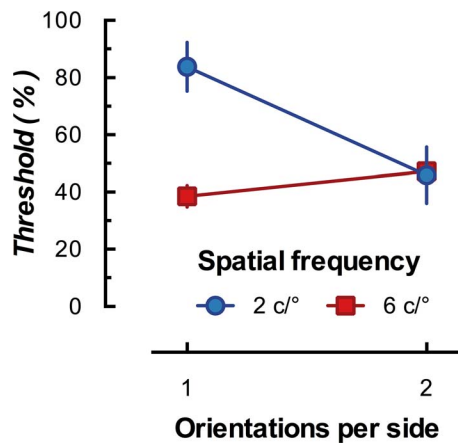


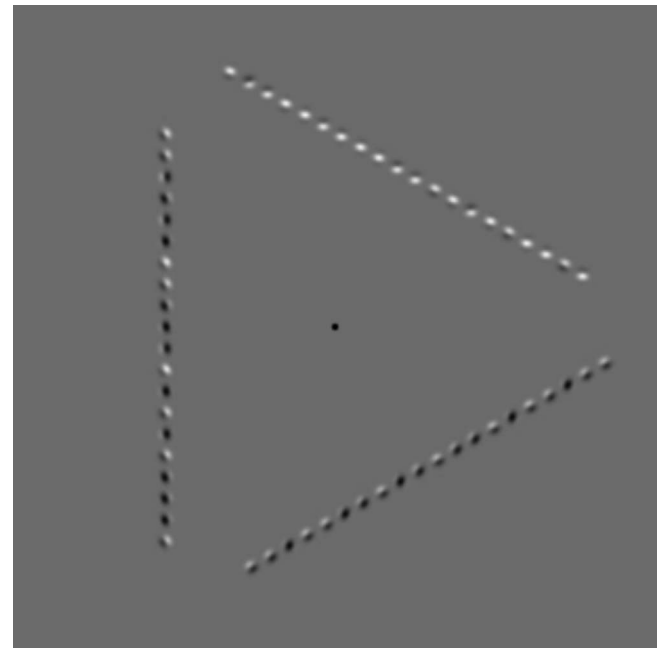
Figure 4. Motion coherence thresholds (75%) for Experiment 3. The stimulus was a triangle in all conditions while the orientations in each side and spatial frequency was varied. The error bars represent ± 1 standard error.

condition regardless of the number of orientations 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) \times 2 (spatial frequency) repeated-measures ANOVA showed that thresholds significantly decreased with increasing number of orientations, $F(1, 2) = 27.84$, $p = 0.03$, $\eta_p^2 = 0.30$. There was no main effect of spatial frequency, $F(1, 2) = 7.42$, $p = 0.11$, $\eta_p^2 = 0.13$, nor a significant interaction, $F(1, 2) = 5.50$, $p = 0.14$, $\eta_p^2 = 0.34$. 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.

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 $+20^\circ$ 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



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.

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 range is small whereas the stimulus integrates when the orientation range is large.

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 $\sim 45^\circ$ 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.

We compared the thresholds in this experiment using a 6 (orientation range) \times 2 (spatial frequency) repeated-measures ANOVA. Thresholds decreased with increasing orientation range for the 2 c/° but not, 6 c/° ,

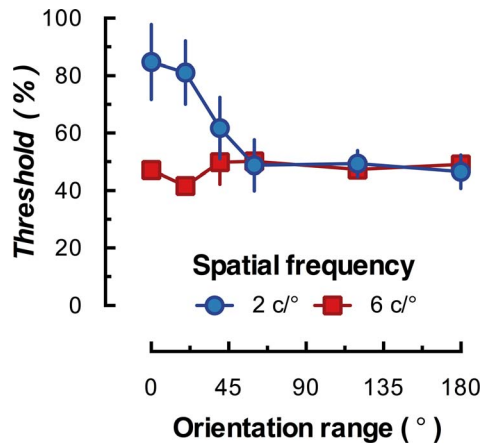
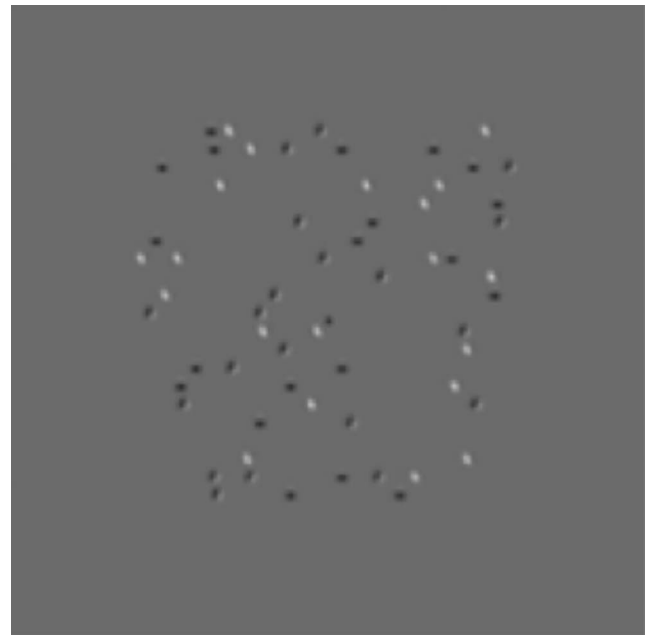


Figure 5. Motion coherence thresholds (75%) for the 2 $c/^\circ$ and 6 $c/^\circ$ stimuli used in Experiment 4. The error bars represent ± 1 standard error.

condition as evidenced by a significant interaction, $F(5, 10) = 4.16$, $p = 0.02$, $\eta_p^2 = 0.27$. Thresholds were also on average higher for the 2 $c/^\circ$ than 6 $c/^\circ$ condition, $F(1, 2) = 25.55$, $p = 0.03$, $\eta_p^2 = 0.19$. Because of the significant interaction, there was no main effect of orientation range, $F(5, 10) = 2.24$, $p = 0.13$, $\eta_p^2 = 0.17$. Follow-up, post-hoc tests (with Bonferroni corrections) showed the spatial frequency conditions (2 vs. 6 $c/^\circ$) were different with 0° and 20° orientation ranges (all $ps < 0.05$), but were statistically indistinguishable at larger ranges (all $ps > 0.05$). The crucial variable for determining whether the occluded shapes are globally integrated appears to be whether a critical range of orientations ($> 40^\circ$) 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).

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 (Lorceau & 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



Movie 7: The peripheral presentation example from Experiment 5. The stimulus contains randomly-distributed Gabors with the orientations being consistent with the four 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.

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

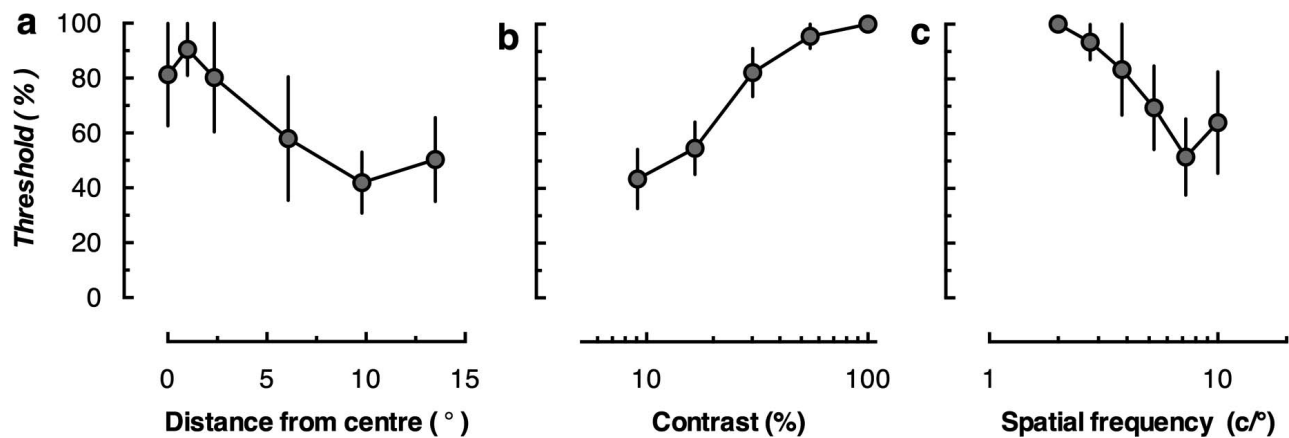


Figure 6. Motion coherence thresholds (75%) measuring the effect of low-level stimulus properties in Experiment 5. The randomly-distributed Gabor stimulus, representing four sides of a diamond (i.e., two motion directions) was used. The error bars represent ± 1 standard error. The stimuli were presented 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/°.

clear sense of either transparency or 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).

We used this stimulus to explore a number of low-level factors that 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 & 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 nonform-based explanation for the effect (Takeuchi, 1998).

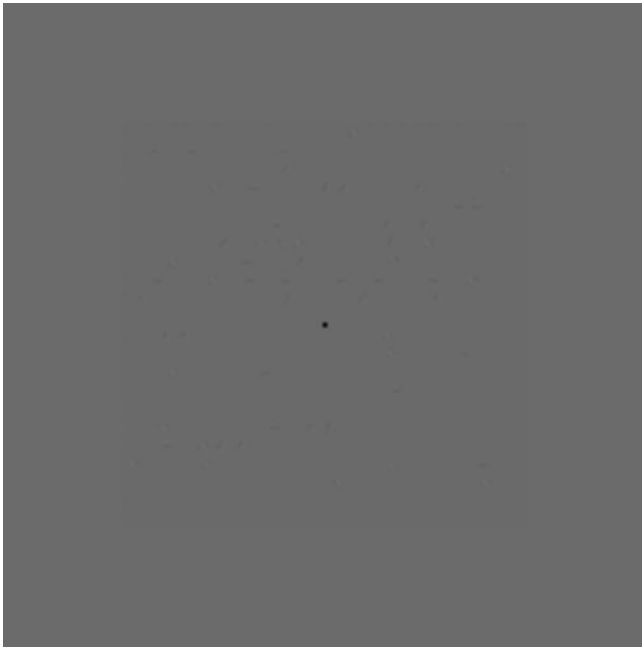
We measured motion integration for the randomly-distributed stimulus at various presentation eccentricities to investigate whether the previous result was due to decreased motion transparency perception. To do this, the stimuli were presented at six distances (0°, 1°, 2.35°, 6.08°, 9.79°, 13.5°) from 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, $F(1, 5) = 4.07$, $p = 0.03$, $\eta_p^2 = 0.67$. Motion integration (with corresponding decrease in transparency), therefore, increases with peripheral presentation.

The next manipulation sought to explain why integration increases for the occluded-aperture stimulus with decreasing contrast (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.

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, $F(1, 4)$

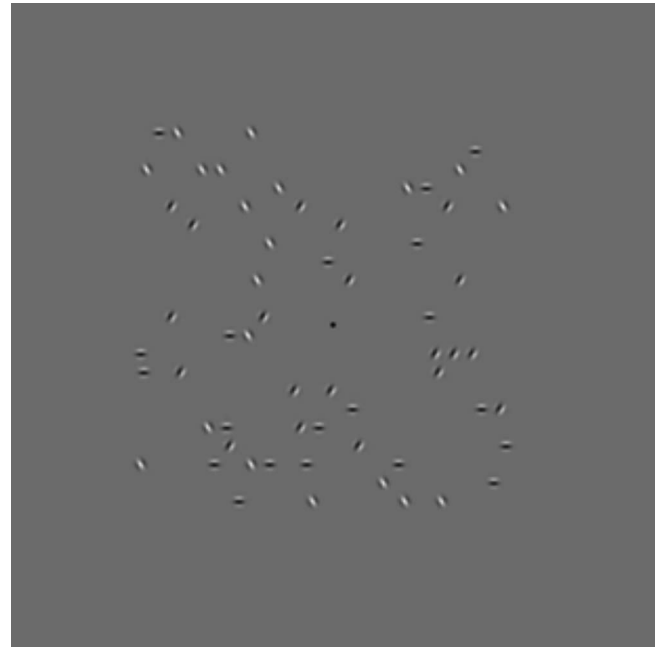


Movie 8: The contrast manipulation from Experiment 5. The stimulus changes from being perceived as the two planes of translation motion to one single, globally-integrated motion as the contrast decreases in each instance. On a gamma-corrected monitor the stimulus contrast will change in logarithmically-spaced steps.

$= 8.51$, $p = 0.006$, $\eta_p^2 = 0.81$. 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 ($6\text{ c}/^\circ$) are integrated in conditions where lower spatial frequency stimuli ($2\text{ c}/^\circ$) 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.

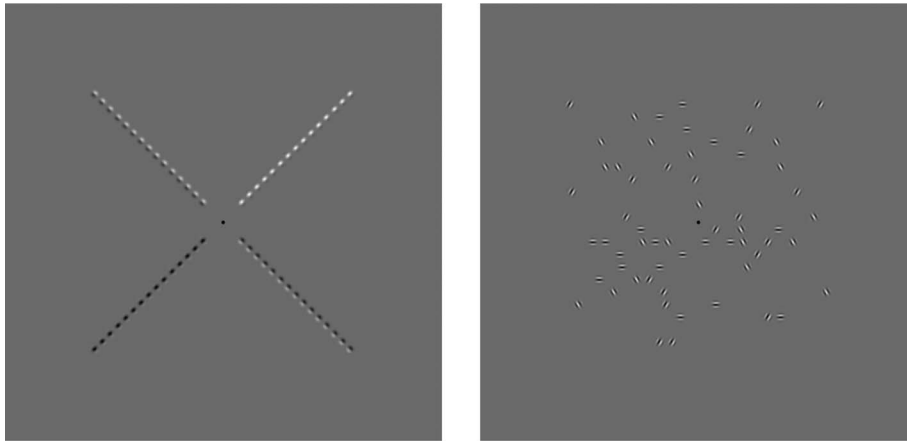
Movie 9 shows the effect of varying the spatial frequency between 2 and $10\text{ c}/^\circ$ in logarithmically-spaced steps on motion transparency. Transparency is evident at lower spatial frequencies, whereas integration dominates at higher spatial frequencies. The spatial frequency of the stimulus 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, $F(1, 5) = 3.40$, $p = 0.047$, $\eta_p^2 = 0.63$. 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 $10\text{ c}/^\circ$ 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.

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-



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.

aperture stimulus rather than the purported high-level or form-based explanations (Lorenceanu & Alais, 2001; Lorenceanu & Shiffrar, 1992; Shiffrar & Lorenceanu, 1996).

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 (Lorenceanu & Alais, 2001). Lorenceanu 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 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., 2009; Kane et al., 2011) 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° (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.

We quantified these effects by measuring the motion coherence thresholds for the open and random stimulus configurations, comparing them to thresholds found for the $2\text{ c}/^\circ$ 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 (Lorenceanu & Alais, 2001), shapes forming open contours were less effectively integrated than shapes forming closed contours. Thresholds for the randomly-distributed Gabors were

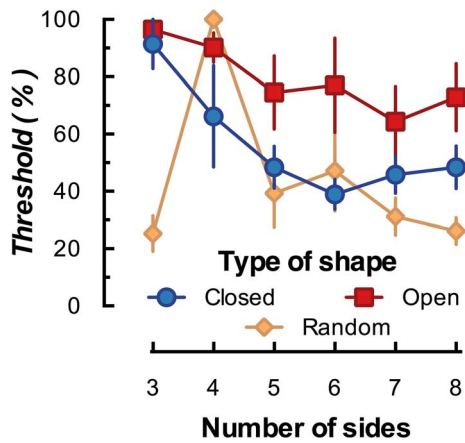


Figure 7. Motion coherence thresholds (75%) measuring the effect of varying the number of sides for closed, open and random conditions in Experiment 5. All stimuli were presented at 2 c° . The error bars represent ± 1 standard error.

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.

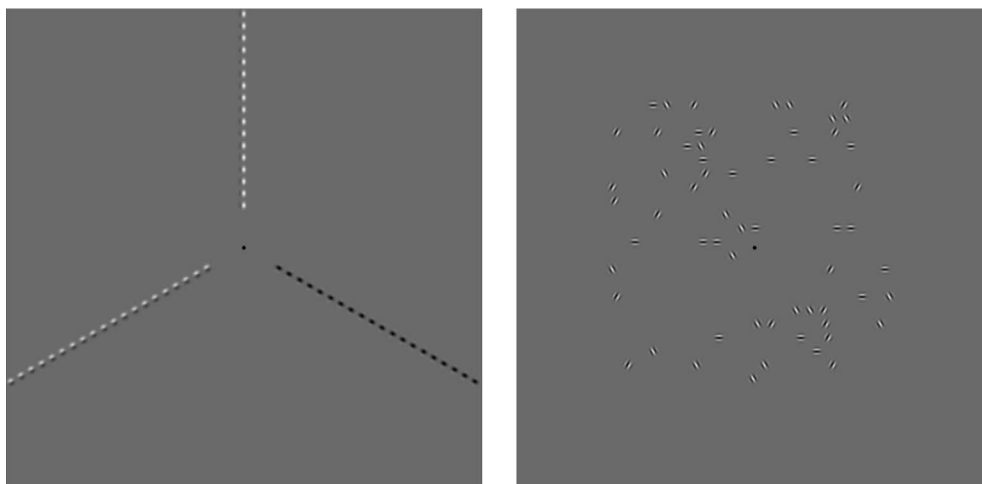
To confirm these observations, we compared thresholds using a 6 (number of sides) \times 3 (shape type) repeated-measures ANOVA. Thresholds significantly changed with an increasing number of sides, $F(5, 10) = 10.27$, $p = 0.001$, $\eta_p^2 = 0.24$, and were different between the shape types, $F(2, 4) = 7.37$, $p = 0.046$, $\eta_p^2 = 0.27$, and there was a significant interaction between number of sides and shape types, $F(10, 20) = 5.33$, $p = 0.0007$, $\eta_p^2 =$

0.23. 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.

Overall, the results 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 (Kane et al., 2009; Kane et al., 2011; Lorenceau & Alais, 2001). Integration occurred in the later studies (Kane et al., 2009; Kane et al., 2011;) 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, & Badcock, 2013, for radial frequency patterns).

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



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.

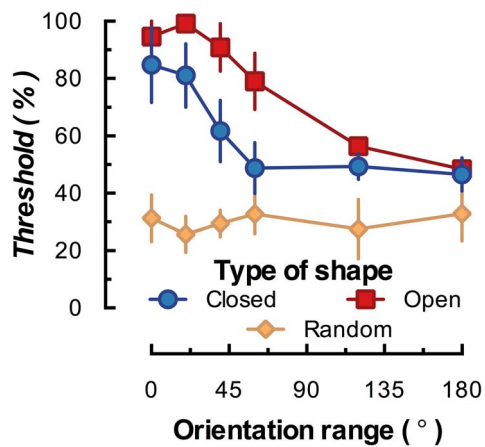


Figure 8. Motion coherence thresholds (75%) measuring the effect of varying the orientation range for closed, open and random conditions in Experiment 7. All stimuli were presented at 2 c°. The error bars represent ± 1 standard error.

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.

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) and 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) \times 3 (shape type) repeated-measures ANOVA confirmed this pattern of results. Thresholds significantly decreased when the orientation range increased, $F(5, 10) = 15.42$, $p = 0.0002$, $\eta_p^2 = 0.16$. Thresholds were also significantly different between the three shape types, $F(2, 4) = 34.32$, $p = 0.003$, $\eta_p^2 = 0.55$, which significantly interacted with orientation range, $F(10, 20) = 3.20$, $p = 0.01$, $\eta_p^2 = 0.12$. These results suggest that any type of contour will become integrated when the orientation range is very large.

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 (Lorenceanu & Alais, 2001; Lorenceanu & Shiffrar, 1992; McDermott & Adelson, 2004; McDermott et al., 2001). The study had two main aims: first, 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 (Lorenceanu & Alais, 2001; Lorenceanu & Lalanne, 2008; Maruya & Nishida, 2010; McDermott & Adelson, 2004; McDermott et al., 2001; Shiffrar & Lorenceanu, 1996) limited the generalizability of the conclusion. This configuration leads to motion directions separated by 90°, the midpoint 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°. 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 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; Kane et al., 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 the 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 article, 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 & Edwards, 2006, 2009). Reducing the contrast, increasing the spatial frequency, peripheral presentation (Lorenceau & Alais, 2001; Lorenceau & Shiffrar, 1992; Shiffrar & Lorenceau, 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 the individual directions represented when the separation between directions decreases, due to the greater overlap in the population response. Conversely, transparency is perceived when there is high certainty of the individual directions because of the large direction separations resulting in differentiable population responses.

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.

Keywords: form-motion interaction, motion integration, transparency, global pooling

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