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The false aperture problem:

Global motion perception without integration of local motion signals

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R.A. designed and conducted the experiments, analyzed and interpreted data, and wrote the article. A.A. provided overall project coordination and proofread the article.

The results of the first experiment were presented at the Vision Science Society conference (Allard & Arleo, 2016b), and the results of the second experiment were presented at the European Conference on Visual Perception (Allard & Arleo, 2016a). This study was not preregistered and the data are available upon request to the corresponding author.

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Abstract

Early direction-selective neurons in the primary visual cortex are widely considered to be the main neural basis underlying motion perception even though motion perception can also rely on attentively tracking the position of objects. Because of their small receptive fields, early direction-selective neurons suffer from the aperture problem, which is assumed to be overcome by integrating inputs from many early direction-selective neurons. Because the perceived motion of objects sometimes depends on static form information and does not always match the mean direction of local motion signals, the general consensus is that motion integration is form-dependent and complex. Based on the fact that early direction-selective neurons respond to motion only within a short temporal window, the current study used stroboscopic motion to test their contribution to motion perception of objects. For conditions under which the perceived motion was impaired by stroboscopic motion, the perceived motion matched the mean direction of local motion signals and was form-independent. For classic conditions under which the perceived motion could not be explained by a simple form-independent averaging of local motion signals, neutralizing the contribution of early direction-selective neurons using stroboscopic motion had little impact on the perceived motion, which demonstrates that the perceived motion relied on position tracking, not on early direction-selective neurons. When the perceived motion relies on position tracking, assuming that motion perception relies on early direction-selective neurons can lead to erroneously postulate the existence of complex or form-dependent integration of inputs from early direction-selective neurons.

Keywords: Motion perception; Aperture problem; Direction-selective neurons; Position tracking; Stroboscopic motion; Global motion

Introduction

Since Hubel and Wiesel (Hubel & Wiesel, 1959, 1962) recorded early direction-selective neurons in the primary visual cortex, such neurons are considered to be the main neural basis underlying motion perception. Early direction-selective neurons are sensitive to motion energy within their receptive fields (Adelson & Bergen, 1985; Emerson, Bergen, & Adelson, 1992) and within a short temporal window (<100 msec; Bair & Movshon, 2004; Baker & Braddick, 1985; Braddick, 1973; Georgeson & Harris, 1990; Morgan & Ward, 1980). However, because their receptive fields are small, they suffer from the famous aperture problem (Adelson & Movshon, 1982; Fennema & Thompson, 1979; Marr & Ullman, 1981; Wallach, 1935; Wuerger, Shapley, & Rubin, 1996): local motion signals are often ambiguous and do not necessarily reveal the global motion direction of the object (e.g., Video 1). The general consensus is that this aperture problem is overcome by integrating local motion signals into a global moving object (e.g., global motion stage in Figure 1), but the precise nature of this integration remains highly debated (see various models cited below). However, here we show that the perceived global direction of simple objects that would generally be assumed to be processed by early direction-selective neurons did not rely on early direction-selective neurons.

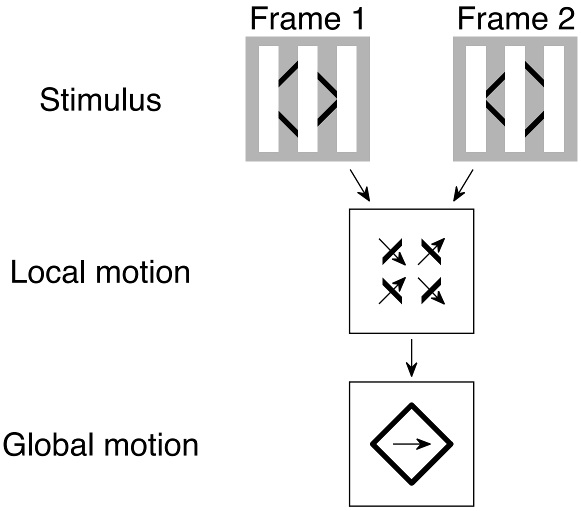

Figure 1. Motion processing based on local motion signals. An object moving in a direction (here a partially occluded black diamond moving from left to right) often induces local motion signals in different directions (aperture problem, Video 1). Local motion signals can be detected by early direction-selective neurons and can be integrated at a global motion stage to solve the aperture problem. Various integration strategies have been suggested (see text).

The simplest motion integration strategy consists in a vector averaging (or summation) of local motion signals detected by early direction-selective neurons (Adelson & Movshon, 1982; Amano, Edwards, Badcock, & Nishida, 2009; Weiss, Simoncelli, & Adelson, 2002). However, the perceived motion direction of an object often does not match the mean direction of local motion signals. A classic example is a drifting tilted line (Wallach, 1935; Wuerger et al., 1996), which can be perceived as moving in its veridical direction when viewed entirely and perceived as moving in a direction orthogonal to the line orientation when viewed through an aperture (Video 1). The difference between the perceived motion direction and the mean direction of local motion signals has led to the general consensus that, at least under some conditions, the aperture problem is overcome by an integration process (i.e., global motion stage in Figure 1) more complex than vector averaging. It has been suggested that the visual system could rely on non-ambiguous local motion signals such as corners or line terminators (extracted by end-stopped cells (Caplovitz & Tse, 2007; Lorenceau, Shiffrar, Wells, & Castet, 1993; Pack, Gartland, & Born, 2004; Pack, Livingstone, Duffy, & Born, 2003; Shimojo, Silverman, & Nakayama, 1989; Ullman, 1979)), select the most reliable local motion signals (Nowlan & Sejnowski, 1995), compute the intersection of constraints (Adelson & Movshon, 1982; Nakayama & Silverman, 1988), compute differentiation between local motion signals (Anstis, 2012; Braddick, 1993) or use predictive coding based on some prior assumptions for the binding of segments (e.g., a regular shape is more probable than a random one) and local motion signals (Perrinet & Masson, 2012).

Furthermore, the perceived motion does not always depend solely on motion information as different stimuli containing the same motion information and differing only on spatial information can result into radically different motion percepts. For instance, the perceived motion direction of a partially occluded object can depend on the disparity (Shimojo et al., 1989), visibility (Lorenceau & Alais, 2001; Lorenceau & Shiffrar, 1992) and shape (McDermott, Weiss, & Adelson, 2001) of stationary occluders. Famously, the global motion percept of a rotating diamond having its corners occluded can be easily perceived when the occluders are visible (e.g., first sequence in Video 4), but not when they blend with the background (Lorenceau & Alais, 2001; Lorenceau & Shiffrar, 1992) (e.g., first sequence in Video 5). Varying the visibility of the stationary occluders by only changing their color or luminance can drastically affect the perceived motion. Furthermore, altering the spatial configuration of moving parts without altering the vector mean of local motion signals can also drastically impair the global motion percept (Lorenceau & Alais, 2001) (e.g., first sequence in movie Video 6). These form-motion interactions were taken as evidence that motion integration (i.e., global motion stage in Figure 1) may not only be complex, it can also be form-dependent as whether the local motion signals are integrated into a global moving object or not would depend on spatial information (e.g., depth, shape, luminance, color and spatial configuration).

In sum, the common assumption that the perceived global motion relies on inputs from early direction-selective neurons led to the general consensus that the aperture problem is sometimes solved by complex or form-dependent integration of local motion signals (Figure 1). Although early direction-selective neurons are assumed to be the main underlying neural basis of motion perception, motion perception does not necessarily rely on early direction-selective neurons as the position of a feature can be attentively tracked (Cavanagh, 1992) and the existence of a position-based motion system that does not rely on early direction-selective neurons is well established (Allard & Faubert, 2013a, 2016; Anstis & Mackay, 1980; Cavanagh, 1992; Lu & Sperling, 2001; Seiffert & Cavanagh, 1998; Smith, 1994; Ullman, 1979). However, tracking a feature faces the same aperture problem as early direction-selective neurons when the motions of features are ambiguous (e.g., global direction of the diamond cannot be inferred by tracking an edge in Figure 1). Thus, motion integration would be required to solve the aperture problem for some stimuli (e.g., Figure 1) whether ambiguous local motion of features is extracted by early direction-selective neurons or tracked. However, there is no reason why the position of a simple feature (e.g., edge) could be tracked, but not the position of a global shape (e.g., diamond, Figure 2). Given that a shape can be localized in space based only on spatial information (e.g., a static shape can be localized in space), the position of the global shape could be tracked in which case the perceived global motion would *not* rely on the integration of local motion signals so there would be no aperture problem to solve. The first experiment of the current study investigated the contribution of early direction-selective neurons and position tracking to the perceived motion of a simple object: a spot. The second experiment investigated which of these motion systems is responsible for the famous form-motion interaction described above and typically taken as evidence of a form-dependent integration of inputs from early direction-selective neurons.

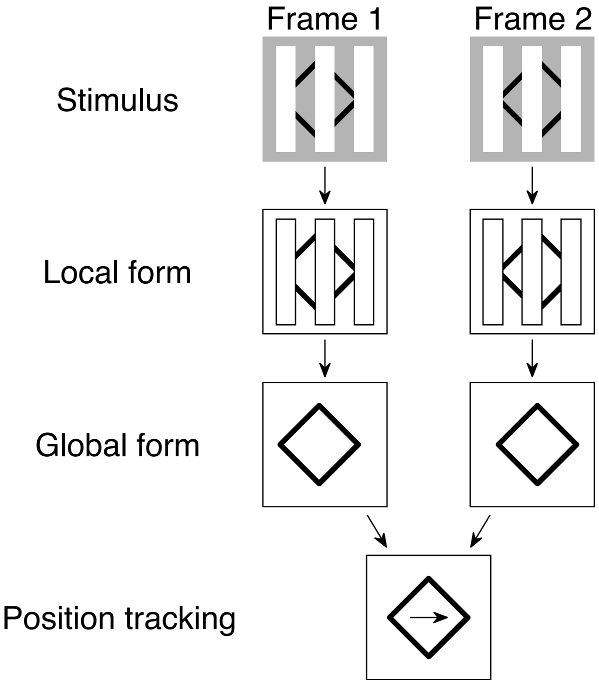

Figure 2. Motion processing based on tracking the position of a global object. The perceived trajectory of an object can be computed without first extracting local motion signals (as in Figure 1). An object can be localized by integrating local form information (e.g., edges) and its global shape can then be tracked.

Experiment 1: Reverse-phi and attentional resolution

The first experiment investigated how we perceive the motion direction of spots rotating around a fixation point (left panel of Figure 3).

Methods

Observers

Seven naïve observers with normal or corrected-to-normal vision participated in each experiment. Only a few participants were necessary because the goal was to objectively confirm strong subjective perceptual effects. Note that the reader can directly experience the strong perceptual effects reported in the results section by viewing the videos provided in supplementary material. The experimental procedures were approved by the Comité de Protection des Personnes Ile de France V in accordance with the Code of Ethics of the World Medical Association (Declaration of Helsinki). Informed consent was obtained from participants prior to the experiment.

Apparatus

Stimuli were presented on a 22.5-inch LCD monitor designed for psychophysics (VIEWPixx) with a refresh rate of 120 Hz. The viewing distance was 50 cm resulting in spatial resolution of 32 pixels per degrees of visual angle (dva). The monitor was the only source of light in the room (50 cd/m^2). The output intensity of each color gun was carefully linearized (gamma correction).

Stimuli and procedure

Observers were asked to report the rotating direction (clockwise or counterclockwise) of spots along an annulus of 8 dva (Figure 3) from a fixation point. The spots were blobs following a windowed cosine function of 1 dva. The ring of spots was rotated by 2.8 degrees (i.e., 0.39 dva) every 150 msec for a duration of 1200 msec. This saccadic motion at 6.7 Hz (1/150 msec) is slightly different from continuous motion, but is nevertheless expected to strongly activate early direction-selective neurons. The lapses between position updates (150 msec) could not be varied over a large range as it needed to be more than 100 msec to enable stroboscopic motion with gaps of at least 100 msec (see below). The rotating speed was maximized by displacing the spots by 2.8 degrees (0.39 dva) at every step, which is a quarter of the smaller distance between spots at the highest density (32 spots). A step size of half the distance between spots would have caused ambiguous motion.

To investigate the contribution of the tracking system, the ability to perceive motion was investigated for different spot densities: 1, 2, 4, 8, 16 and 32 spots uniformly distributed on an annulus. Position tracking is inefficient when the number of feature to attend is above the spatial resolution of attention (Allard & Faubert, 2013a, 2016), which corresponds to about 14 spots distributed on an annulus (Intriligator & Cavanagh, 2001).

To investigate the contribution of the energy-based motion system, two manipulations were performed. The contrast polarity of the spots (black or white) was either constant during a trial (i.e., phi motion), or alternated at each displacement causing motion energy to be reversed (i.e., reversed-phi motion; Anstis, 1970; Anstis & Rogers, 1975), which reverses the preferred motion direction of early direction-selective neurons (Clark, Bursztyn, Horowitz, Schnitzer, & Clandinin, 2011; Emerson, Citron, Vaughn, & Klein, 1987; Livingstone & Conway, 2003). The second manipulation consisted in presenting the spots continuously during the trial or stroboscopically (25 msec followed by a 125 msec temporal gap) as illustrated in Figure 3. In both cases, the spots were displaced every 150 msec. Early direction-selective neurons are known to be sensitive to energy motion occurring within their receptive fields and within a temporal window shorter than about 100 msec (Bair & Movshon, 2004; Baker & Braddick, 1985; Braddick, 1973; Georgeson &

Harris, 1990), so a temporal gap of 125 msec neutralizes (or at least severely compromise) their contribution to motion perception.

The resulting 24 conditions (6 spot densities times 2 types of motion (phi or reversed-phi) times 2 display conditions (continuous or stroboscopic)) were each presented 5 times in a pseudo-random order within a block. Each observer performed 8 blocks of trials for a total of 40 trials per condition.

This study was not preregistered and the data are available upon request to the corresponding author.

Results & discussion

When the spot density was considerably below attentional resolution (up to 4 spots, see Figure 3 and Video 2), motion was perceived in their veridical direction: reversing energy direction (i.e., reverse-phi motion) and/or compromising the contribution of motion detectors sensitive to motion only within a short temporal window (i.e., stroboscopic motion) had little impact on the perceived motion direction (performance near 100% in all cases). Results were drastically different when the spot density was considerably above attentional resolution (i.e., 32 spots, see Video 3) in which case reversing energy direction reversed the perceived motion direction (performance near 0%, filled grey symbols in Figure 3) and stroboscopic motion compromised motion perception (performance near chance, open symbols). Although the distance between spots was the lowest in the 32-spot configuration, lateral interaction (e.g., Chemla et al., 2019) between spots is unlikely the cause because the distance was nevertheless relatively large (1.57 dva) and the results were expected based on the properties of early direction-selective neurons (reverse-phi reverses their preferred response direction and their temporal window is shorter than 100 msec).

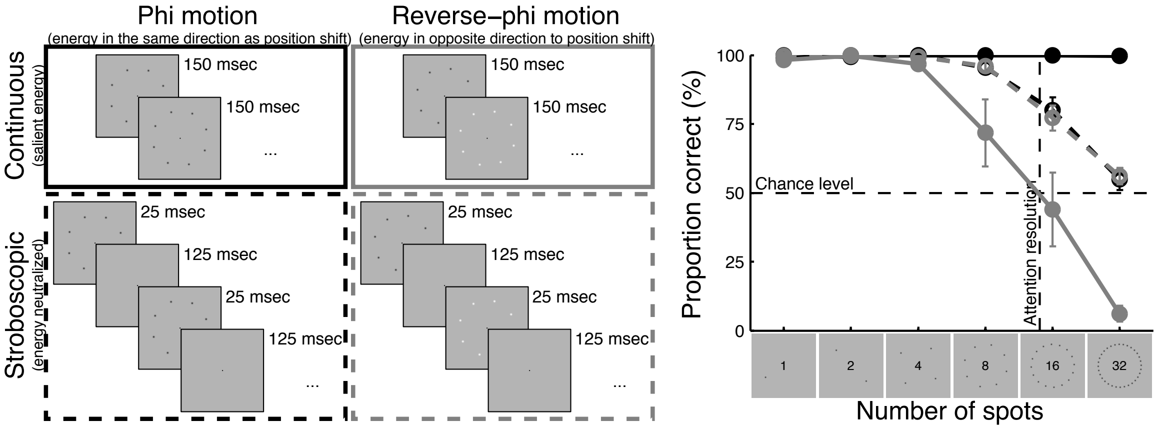

Figure 3. Perceived motion direction of apparent motion. Left panel represents the four motion conditions, each tested with 1, 2, 4, 8, 16 and 32 spots uniformly distributed around an annulus of 8 degrees of visual angle of eccentricity. Right panel represents the results averaged across observers. Filled and open symbols represent continuous and stroboscopic motion, respectively. Black and grey symbols represent phi motion (constant contrast polarity) and reverse-phi motion (alternating contrast polarity at each motion displacement), respectively. Error bars represent standard error of the mean (lower than symbols where not visible). Perceiving motion in the opposite direction as the position displacement would have resulted in a performance at 0%. Perceiving no net motion would have resulted in performance near chance (dashed thin horizontal line). Dashed thin vertical line represents approximated attentional resolution (Intriligator & Cavanagh, 2001).

The fact that no motion was perceived with 32 spots under stroboscopic stimulation (performance near chance and observers reported no motion sensation as can be appreciated in the second and fourth sequences of Video 3) implies that the contributions of direction-selective neurons and position tracking were both negligible in these conditions. Presenting the same 32-spot stimuli continuously led to perceived motion in the energy direction: phi motion was perceived in the veridical direction (first sequence in Video 3, black solid line in Figure 3) and reverse-phi motion (Anstis, 1970; Anstis & Rogers, 1975) was perceived in the opposite direction (third sequence in Video 3, grey solid line in Figure 3). The fact that no motion was perceived with 32 spots under stroboscopic stimulation and motion was perceived in the energy direction under continuous stimulation, confirms that stroboscopic motion successfully impaired the contribution of early direction-selective neurons. Indeed, these results are consistent with the facts that early direction-selective neurons operate within a short temporal window (Bair & Movshon, 2004; Baker & Braddick, 1985; Braddick, 1973; Georgeson & Harris, 1990; Morgan & Ward, 1980) and that reverse-phi indeed reverses their direction selectivity (Clark et al., 2011; Emerson et al., 1987; Livingstone & Conway, 2003). Thus, there is no doubt that early direction-selective neurons were the neural basis underlying motion perception in the continuous 32-spot conditions (as generally assumed) and that stroboscopic motion compromised the contribution of early direction-selective neurons (as expected).

Given that early direction-selective neurons did not considerably contribute to motion perception under stroboscopic stimulation, stroboscopic motion can be used to estimate the contribution of a position tracking strategy. Position tracking considerably contributed to motion only when the spot density was considerably below attentional resolution of about 14 elements (Intriligator & Cavanagh, 2001). Indeed, when the contribution of early direction-selective neurons was minimized (stroboscopic motion, open symbols in Figure 3), motion was correctly perceived when the spot density was lower than attentional resolution (i.e., up to 4 or 8 spots depending on participants; Video 2) and not when density was considerably above attentional resolution (i.e., 32 spots; Video 3). These results show that position tracking considerably contributed to motion perception only when spot density was markedly below attentional resolution, which is consistent with previous findings (Allard & Faubert, 2013a, 2016).

Consequently, continuous reverse-phi motion was perceived as moving in its veridical direction up to 4 or 8 spots, and perceived in the opposite direction with 32 spots. With 32 spots, motion was perceived in the opposite direction undeniably because reverse-phi reverses the direction selectivity of early direction-selective neurons (Clark et al., 2011; Emerson et al., 1987; Livingstone & Conway, 2003). Up to 4 or 8 spots, however, the perceived motion relied on position tracking as motion was perceived in the veridical direction, not the preferred direction of early direction-selective neurons. These results therefore suggest that an object can be attentively tracked despite its polarity flickering over time, which is consisting with the fact that tracking can operate despite the object changing its color and shape (Cavanagh, Arguin, & von Grünau, 1989; Kolers & Pomerantz, 1971; Kolers & von Grünau, 1976). Around the attentional resolution (i.e., 16 spots), there was a high inter-subject variability (large error bars in Figure 3) compared with the stroboscopic conditions. Interestingly, in this condition, the two motion systems would similarly contribute to motion, but in opposite directions. The high inter-subject variability suggests different observers had considerably different thresholds at which the contribution of the two motion systems would be counterbalanced. Note that although performance is near chance level, it does not imply that no motion was perceived (as for stroboscopic motion at 32 spots) as motion perception could be perceived in both directions (i.e., transparent motion) or a bistable motion percept could be perceived (alternating directions).

Note that the current experiment was conducted under some specific parameters. The eccentricity was set to 8 dva, but the findings likely generalize to a wide range of eccentricity for a given number of spots as spatial resolution scales with eccentricity (Intriligator & Cavanagh, 2001; e.g., viewing Videos 2 and 3 at different distances has little impact on the perceived motion). Also, saccadic motion was used instead of continuous motion, but the results confirm that this stimulus causes a strong motion response in early direction-selective neurons as the observers could easily discriminate the direction of motion when the contribution of position tracking was neutralized with 32 spots (performance at 100%). The use of this saccadic motion, which was necessary for stroboscopic and reverse-phi motion, forced the use of a relatively slow speed (2.6 dva/s) so it is not possible to know if the perceptual effects would generalize to higher speeds. Nonetheless, we should expect the contribution of position tracking to decrease with increasing speed.

Experiment 2: Motion integration

In the second experiment, we investigated how local information is integrated into a global moving object using a stimulus classically used to probe motion integration: a rotating diamond with static occluders hiding its corners (Lorenceau & Alais, 2001; Lorenceau & Shiffrar, 1992; McDermott et al., 2001). As in the first experiment, stroboscopic motion was used to neutralize the contribution of early direction-selective neurons. To minimize the contribution of a position tracking strategy, the same stimuli were viewed peripherally where tracking relatively small position displacements is difficult (Allard & Faubert, 2016).

Method

Observers

The same observers participated to the second experiment.

Apparatus

The same apparatus was used with the exception that the viewing distance was 100 cm resulting in spatial resolution of 64 pixels/dva.

Stimuli and procedure

Observers were asked to discriminate the rotating direction (clockwise vs counterclockwise) of the position of a shape by pressing one of two keyboard keys. The stimuli for continuous motion were similar to the ones used in previous studies (Lorenceau & Alais, 2001; Lorenceau et al., 1993), but we used smaller stimuli and smaller amplitude of motion to facilitate the neutralization of position tracking in peripheral vision. The stimulus was visible for 1100 msec during which the shape rotated by a complete cycle around a radius of 0.0625 dva (i.e., ~ 3 minutes of arc = 4 pixels), with a random initial global position. The corners of the shape were occluded by three vertical occluders. Given that each line segment was perceived through a narrow opening between two occluders, the motion of a single line was ambiguous (i.e., aperture problem, Video 1) and perceiving the global motion therefore required some integration. It has been shown (Lorenceau & Alais, 2001) that the perception of the global motion depends on the visibility of the occluders and the shape of the moving object. The visibility of the occluders was altered by changing their brightness, which was either grey (50 cd/m^2, in which case they fused with the background) or light grey (55 cd/m^2). The baseline shape was a diamond (more precisely, a square rotated by 45 degrees) to which the distance between two parallel segments was 2 dva. Two shapes were used: a closed shape (i.e., diamond) and an open shape (i.e., chevron (Lorenceau & Alais, 2001)), which was obtained by swapping the positions of the two bottom lines. The line segments of the rotating shape were black with a width profile following a windowed cosine function of 0.3 dva. The size of the occluders was 0.75 by 3.6 dva separated by gaps of 0.67 dva so that the center of the occluders were in line with the mean left, center and right corner positions.

To investigate the contribution of energy-based processing, motion was either continuous (displaced every 33 msec) or stroboscopic (appeared for 33 msec with 100 msec gaps). The global motion speed was kept constant to 0.9375 Hz in both cases so that the object was moved by a complete cycle during the 1100 msec presentation.

To investigate the contribution of the position tracking motion system, the stimulus was viewed either at fixation or at 20 degrees of eccentricity to the right of a fixation point. Position tracking of oscillating motion over a short spatial range is undeniably more difficult in the periphery (Allard & Faubert, 2016), which was confirmed by the results presented below.

In sum, there were 4 binary independent variables resulting into 16 conditions: shape of the object (diamond/chevron), brightness of the occluders (visible/invisible), motion type (continuous/stroboscopic) and eccentricity (central/peripheral). To avoid position uncertainty, eccentricity was constant within a block. To avoid triggering strong transients not related to the moving stimulus, the occluders were constantly displayed throughout a block (even between trials) and its brightness did not vary within a block. The other two variables (shape and motion type) were interlaced within blocks resulting into 4 different blocks (visible/invisible occluders X central/peripheral) each interlacing 4 different conditions (diamond/chevron X continuous/stroboscopic). A block was composed of 80 trials in which the 4 conditions were presented 20 times in a random order. Each of the four blocks was performed twice in a pseudo-random order, resulting in a total of 40 trials for each of the 16 conditions.

Results & discussion

The results were consistent with the known form-motion interaction taken as evidence that spatial information affects motion integration (Lorenceau & Alais, 2001; Lorenceau & Shiffrar, 1992): the global motion of the continuously rotating diamond viewed centrally was easily perceived when the occluders were visible (first light-grey column in Figure 4, first sequence in Video 4), but not when they were invisible (same brightness as the background) or when the spatial configuration was altered to form an open shape (second to fourth light-grey columns, first sequences in Videos 5 to 7; note that for open shapes, discriminating the global motion direction seems easier in the videos than in the testing conditions with a shorter presentation time and interlaced with other conditions). Critically, however, a similar form-motion interaction was also observed under stroboscopic stimulation compromising the contribution of early direction-selective neurons (dark-grey columns, second sequences of the same movies). Thus, the global motion percept depended critically on form information (i.e., brightness of occluders and spatial configuration) and not on the type of motion (i.e., continuous vs stroboscopic).

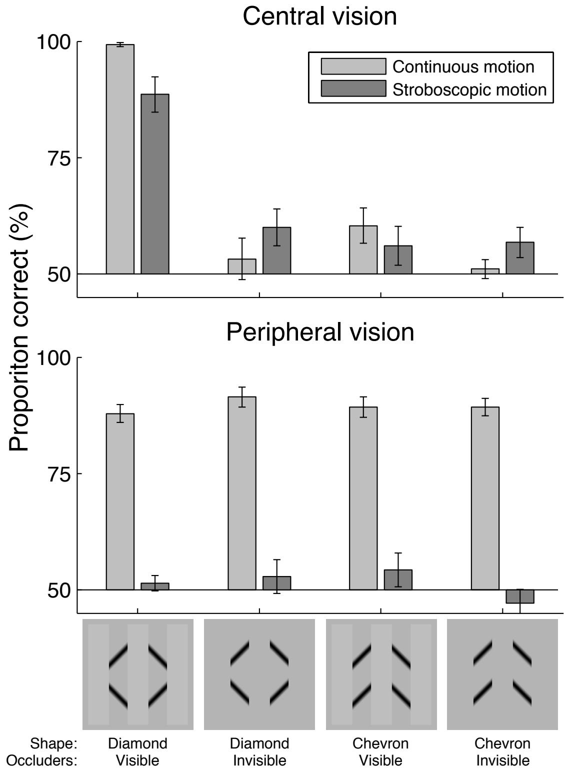

Figure 4. Perceived motion direction requiring integration of local information. Proportion of correct answers (mean across observers) for judging the rotating direction of various stimuli (diamond and chevron shapes with visible and invisible occluders; see Videos 4 to 7). Error bars represent standard error of the mean. Perceiving no motion would have resulted in performance near chance (50%, horizontal line).

The opposite pattern of results was observed when the same stimuli were viewed peripherally where tracking relatively small position displacements is difficult (Allard & Faubert, 2016) (bottom graph of Figure 4). Global motion was efficiently perceived for continuous motion (light-grey columns), but not for stroboscopic motion (dark-grey columns), whether the occluders were visible or not and for the two shape configurations. Thus, in central vision, the perception of global motion strongly depended on form information for both types of motion, whereas in the peripheral vision, the perception of global motion critically depended on the type of motion and was independent of form information.

This double dissociation confirms that stroboscopic motion impaired the contribution of early direction-selective neurons and presenting the stimulus in the periphery impaired position tracking. Indeed, when stroboscopic motion was viewed peripherally, no motion was perceived (dark-grey columns in bottom graph of Figure 4), which can be appreciated by peripherally viewing the second sequences of Videos 4 to 7. This absence of motion perception implies that the contribution of early direction-selective neurons and position tracking to the global motion percept were both negligible. On the other hand, motion was efficiently perceived when presenting the same stimuli continuously (light-grey columns, first sequences of same movies), which indisputably results from the contribution of early direction-selective neurons as generally assumed. When early direction-selective neurons were not contributing to motion (stroboscopic motion), rotation of the diamond with visible occluders was easily perceived at fixation (first dark column, top graph), but not in the periphery (first dark column, bottom graph), implying that the tracking efficiently operated at fixation, but not in the periphery.

Given that some properties of early direction-selective neurons vary with eccentricity, it is tempting to wonder if these differences could explain the different patterns of results observed between central and peripheral vision. However, different properties in early direction-selective neurons cannot explain the differences observed between central and peripheral vision because the perceived motion in central vision did not rely on early direction-selective neurons. Indeed, one property of early direction-selective neurons that does not vary with eccentricity is their temporal integration time (Baker & Braddick, 1985), so that stroboscopic vision with temporal gaps of at least 100 msec neutralizes the contribution of early direction-selective neurons in central and peripheral vision (as confirmed in peripheral vision, see above). Indeed, the results strongly suggest that the perceived motion in central vision relied on position tracking, not early direction-selective neurons. Nevertheless, it could be useful to neutralize position tracking in central vision where the perceived motion is form-dependent. This could be done using high temporal frequencies above the temporal resolution of attention (Allard & Faubert, 2013b) or using a spatially dense stimulus such as concentric diamonds.

Note that Lorenceau and Alais (2001) obtained a similar pattern of results with continuous motion (perceived motion was form-dependent in central vision and not in peripheral vision) using different stimulus parameters: their stimuli were larger, the rotation amplitude was greater, different speeds were evaluated and the peripheral stimulus was presented at a lower eccentricity (12 dva compared with 20 dva in the current study). Thus, although the current study did not investigate over a large set of parameters, the effects likely generalize over a wide range of parameters.

General discussion

With continuous motion under conditions in which position tracking was expected to efficiently operate (i.e., up to 4 spots in experiment 1 and in central viewing in experiment 2), the perceived motion critically depended on form information (brightness of occluders and spatial configuration in experiment 2) and not on the direction of motion energy (phi vs reverse-phi in experiment 1). Neutralizing the contribution of early direction-selective neurons using stroboscopic motion under these conditions had little impact on the perceived motion as the perceived motion also critically depended on form information and not on the direction of motion energy. These results reveal the existence of a motion system that does not rely on early direction-selective neurons (position tracking) and is form-dependent. Conversely, under conditions in which the contribution of position tracking was expected to be neutralized (32 spots in experiment 1 and peripheral viewing in experiment 2), the perceived motion was independent of form information (experiment 2) and critically depended on the direction of motion energy (experiment 1). The fact that no motion was perceived when neutralizing the contribution of early direction-selective neurons using stroboscopic motion under these conditions (both experiments) confirms that the visual system relied on early direction-selective neurons as generally assumed.

The widely held assumption that the visual system relies on early direction-selective neurons to judge the motion direction of objects can lead to a false aperture problem when the visual system rather mainly relies on position tracking: how are inputs from early direction-selective neurons integrated to explain the perceived motion direction of objects? Forcing a solution to this false problem could lead to erroneously postulate the existence of some kind of integration of inputs from early direction-selective neurons. For instance, consider the continuous motion conditions for which the perceived motion cannot be explained by a simple vector averaging of inputs from early direction-selective neurons: continuous motion up to 4 spots in experiment 1 and continuous motion viewed centrally in experiment 2. Assuming that the perceived motion direction relied on early direction-selective neurons would have led to the conclusion that the integration of inputs from early direction-selective neurons must be complex (i.e., not a simple averaging of inputs from early direction-selective neurons) to explain the perceived motion in the veridical direction even when the motion energy is reversed (experiment 1) and must be form-dependent to explain that the perceived motion depended on spatial information (experiment 2) as famously inferred (e.g., a form-based veto on motion integration; Lorenceau & Alais, 2001). However, the same patterns of results were observed when the contribution of early direction-selective neurons was neutralized with stroboscopic motion, which reveals the existence of another motion system (position tracking) that is form-dependent and independent of the direction of motion energy. Before investigating how inputs from early direction-selective neurons are integrated to explain the perceived motion, it is first necessary to determine if the perceived motion relies on early direction-selective neurons. The results in the current study show that, for many simple moving stimuli, the widely held assumption that the perceived motion relies on early direction-selective neurons is questionable and cannot be taken for granted a priori. If the perceived motion does not rely on early direction-selective neurons, then the question of how inputs from early direction-selective neurons are integrated to explain the perceived motion is a false problem.

As mentioned in the introduction, a classical example of the aperture problem is a drifting tilted line (Video 1). When the line is perceived as moving in its veridical direction (e.g., horizontally when viewing the entire line in Video 1), the perceived motion cannot be explained by a simple vector averaging of inputs from early direction-selective neurons, as the mean of local motion signals is oblique. Indeed, the motion direction of a drifting line viewed through an aperture is ambiguous as it is consistent with many motion directions ranging over 180 degrees, but the perceived motion direction through an aperture is usually perpendicular to the line (e.g., oblique motion is perceived when viewing the line through an aperture in Video 1). Based on the assumption that the perceived motion relies on inputs from early direction-selective neurons, this example is typically taken as compelling evidence of an integration process more complex than vector averaging. However, neutralizing the contribution of early direction-selective neurons with stroboscopic stimulation has little impact on the perceived motion (see Video 8), which implies that the veridical motion direction of the line can be perceived by tracking its position. As a result, there is a motion system that does not rely on early direction-selective neurons and that can extract the veridical motion direction of the tilted line, so this classical example does not necessarily imply the existence of complex integration of inputs from early direction-selective neurons.

The furrow illusion (Anstis, 2012) has also been taken as evidence of complex integration of local motion signals. In the furrow illusion, a spot moves in a direction that differs from the mean local motion signals. In central vision, motion is perceived in the veridical motion direction, whereas in the periphery, motion is perceived in the direction of the mean local motion signals. The illusion in the periphery is trivial to explain and is not disputed: the motion percept is the result of a simple vector averaging of inputs from early direction-selective neurons. For central vision, Anstis (2012) concluded that the perceived veridical motion must be the result of a complex integration of inputs from early direction-selective neurons. This conclusion is based on the implicit assumption that the perceived motion relies on the integration of inputs from early direction-selective neurons. However, motion can be perceived in the veridical direction even when neutralizing the contribution of early direction-selective neurons with stroboscopic motion (Allard & Faubert, 2016), which implies the existence of a motion system that does not rely on early direction-selective neurons and can extract the veridical motion direction of the spot. Furthermore, Allard and Faubert (2016) found that using a stimulus configuration that impairs position tracking (crowding) enhanced the furrow illusion, which suggests that position tracking plays an important role in perceiving the veridical motion direction. Consequently, in the furrow illusion, there is no need to postulate the existence of complex integration of inputs from early direction-selective neurons to explain the perceived veridical motion in central vision because there is another motion system (position tracking) that can explain it.

In sum, in these examples (reverse-phi stimulus up to 4 spots, form-dependent rotating square in central vision, drifting tilted line, furrow illusion in central vision), similar motion phenomena were observed when neutralizing the contribution of early direction-selective neurons with stroboscopic motion. These results demonstrate that there is another motion system that does not rely on early direction-selective neurons (position tracking) responsible for these motion phenomena so they do not imply the existence of a particular kind of integration of inputs from early direction-selective neurons. To prove the existence of some kind of integration of inputs from early direction-selective neurons, it is necessary to demonstrate that the motion phenomenon cannot be explained by another motion system (e.g., position tracking). The perceived motion cannot simply be assumed a priori to rely on early direction-selective neurons.

The ideal stimulus to probe the integration of inputs from early direction-selective neurons is therefore one that cannot be processed by position tracking. Interestingly, the current study did not find evidence that the integration of inputs from early direction-selective neurons was complex or form-dependent. Consider the conditions under which only position tracking was neutralized: continuous motion with 32 spots in experiment 1 and continuous motion with peripheral viewing in experiment 2. Observers perceived motion in the mean direction of motion energy (experiment 1) and the perceived global motion was form-independent (experiment 2). Consequently, when the perceived motion was not based on position tracking, the perceived motion relied on the integration of inputs from early direction-selective neurons (as generally assumed), but motion integration was simple (e.g., vector average) and form-independent. In other words, when the visual system necessarily relied on early direction-selective neurons, the solution to the aperture problem simply consisted in averaging the inputs from early direction-selective neurons; we found no evidence of complex or form-dependent integration of inputs from early direction-selective neurons. However, the current study investigated a limited number of conditions, which is not sufficient to conclude that there is no complex or form-dependent integration of inputs from early direction-selective neurons. There may be other conditions that could reveal the existence of complex or form-dependent integration.

Although the perceived motion sometimes clearly relies solely on the contribution of early direction-selective neurons or position tracking, both could contribute to the perceived motion in other conditions. The combination of both contributions could take different forms. The contribution of one motion system could dominate (e.g., continuous reverse-phi motion up to 4 spots in experiment 1 is dominated by position tracking). Conflicting motion interpretations could also result in transparent motion in which both motion percepts are superimposed (e.g., Solomon & Sperling, 1994) or the motion the perceived motion could be bistable, alternating between the two possible interpretations (which is the subjective impression we observed when viewing the reverse-phi stimulus with 16 spots). When the two motion interpretations are not incompatible, the visual system could combine them (e.g., furrow illusion that gradually shifts from position tracking in central vision to early direction-selective neurons in peripheral vision (Allard & Faubert, 2016)). The visual system may also try to combine the two interpretations and apply a drastic correction when the resulting percept diverges too much from reality (e.g., peripheral reverse-phi motion, Lorenceau & Cavanagh, 2020).

In a recent review, Shiffrar (2017) concludes that the solution to the aperture problem often involves a form-dependent integration of local motion signals. The strongest evidence for this claim was the rotating diamond showing that the perceived global motion percept is form-dependent (i.e., second experiment of the current study with continuous motion in central vision).

Based on the implicit assumption that the perceived global motion relied on the integration of inputs from early direction-selective neurons, this form-dependent motion perception was therefore taken as evidence of a form-dependent integration of local motion signals: the global form interpretation of the stimulus (global form stage in Figure 2) would affect the integration of local motion signals (global motion stage in Figure 1). As described above, however, the current study found that the perceived form-dependent global motion for a similar stimulus was based on position tracking, which does not require motion integration, so these results cannot be taken as evidence of a form-dependent integration of local motion signals.

The fact that the global motion percept based on position tracking was form-dependent is not surprising as the ability to track the position of a global shape (Figure 2) obviously depends on the ability to perceive the global shape. The diamond was perceived as a global moving shape when the occluders were visible and as four independent segments when the occluders were invisible (Videos 4 and 5, respectively), which shows that the visibility of occluders affected the global *form* interpretation of the stimulus. When the global form integration stage interpreted the stimulus as a single global shape (diamond; Video 4), then tracking the position of the global shape was easy, but when the global form integration stage rather interpreted the stimulus as four independent segments or two pairs of segments (Video 5), then there was no unified global percept and tracking the position of an unperceived global shape was meaningless (and hard). Consequently, the fact that the perceived motion of a global shape depends on the form interpretation of the global shape would have been surprising if the visual system relied on early direction-selective neurons (because it implies that form processing affects motion integration), but is trivial to explain given that the visual system relied on position tracking (because we cannot track a global shape that is not perceived).

Since tracking the position of a global object does not necessarily require the integration of local motion signals (e.g., Figure 2), sometimes there may be no aperture problem to solve. Indeed, the famous aperture problem is known to be a consequence of the properties of early direction-selective neurons having small receptive fields (i.e., apertures). If the perceived motion of an object is based on tracking its global shape, then it does not rely on the integration of local motion signals so there is no aperture problem to solve. In such a case, the perceived motion would not rely on motion integration, but on form integration enabling to localize an object, and the critical processing stage regarding the motion perception of objects would not be motion integration, but form integration. Since we can localize static objects, the existence of a global form integration process is undeniable, but how objects are localized in space is beyond the scope of the present study.

In conclusion, early direction-selective neurons suffer from the famous aperture problem. Based on the assumption that early direction-selective neurons are the underlying neural basis for judging the motion direction of objects, the consensus is that the integration of inputs from early direction-selective neurons is complex and form-dependent. However, the current study found that for stimuli classically used to provide evidence of complex and form-dependent integration of inputs from early direction-selective neurons, neutralizing the contribution of early direction-selective neurons using stroboscopic motion had little impact on the perceived motion direction, which demonstrates the existence of a motion system that does not rely on early direction-selective neurons (e.g., position tracking) and explains the perceived motion. Note that the current study suggests that the motion system that does not rely on early direction-selective neurons could simply consists in tracking the position of an object localized by the spatial system, which we refer to as position tracking (Figure 2). Indeed, given that a shape can be localized in space based only on spatial information (e.g., a static shape can be localized in space), the position of an object should be easy to track. Nonetheless, other motion models that are not based on early direction-selective neurons are also possible such as feature tracking (e.g., Seiffert & Cavanagh, 1998), attention-based tracking (Cavanagh, 1992), saliency-based (third-order) motion system (Lu & Sperling, 2001), or long-range suppressive waves (Chemla et al., 2019). On the other hand, for particular conditions under which motion perception undeniably relied on early direction-selective neurons, no complex or form-dependent motion integration was observed, which suggests that, for the stimuli used in the current study, the integration of inputs from early direction-selective neurons was simple and form-independent. The aperture problem (how are inputs from early direction-selective neurons integrated to explain the global motion percept?) is a false problem if the perceived global motion does not rely on the integration of local motion signals (e.g., tracking the position of an object).

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Supplementary Information

Video 1. Aperture problem

Through an aperture, the motion direction of a line is ambiguous and is usually perceived in a direction orthogonal to its orientation (here diagonally, first sequence). Without the aperture, the line is usually perceived as drifting in its veridical direction (here horizontally, second sequence). Early direction-selective neurons are sensitive to motion within a small receptive field equivalent to a small aperture. Assuming that the perceived motion of the line is based on early direction-selective neurons sensitive to motion orthogonal to the line, the aperture problem consist in determining how the visual system recover the veridical motion direction.

Video 2. Four rotating spots

The motion was either forward phi-motion (first two sequences) or reverse-phi motion (last two sequences), and either continuous (first and third sequences) or stroboscopic (second and fourth sequences). Observers had to report the rotating direction (here, always clockwise).

Video 3. Thirty-two rotating spots

Legend as in Video 2, but for 32 spots.

Video 4. Rotating diamond with visible occluders

The motion was either continuous (first sequence) or stroboscopic (second sequence). Observers had to report the rotating direction of the global shape position (here, always clockwise).

Video 5. Rotating diamond with invisible occluders

Legend as in Video 4, but with occluders the same brightness as the background.

Video 6. Rotating chevron with visible occluders

Legend as in Video 4, but for a chevron shape.

Video 7. Rotating chevron with invisible occluders

Legend as in Video 4, but for a chevron shape with occluders the same brigthness as the background.

Video 8. Drifting tilted line

Oblique line drifting to the right. The motion is continuous and stroboscopic (first and second sequence, respectively).