Rotational and translational motion interact independently with form

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ABSTRACT

Do the mechanisms that underlie the perception of translational and rotational object motion show evidence of independent processing? By probing the perceived speed of translating and/or rotating objects, we find that an object's form contributes in independent ways to the processing of translational and rotational motion: In the context of translational motion, it has been shown that the more elongated an object is along its direction of motion, the faster it is perceived to translate; in the context of rotational motion, it has been shown that the sharper the maxima of curvature along an object's contour, the faster it appears to rotate. Here we demonstrate that such rotational form–motion interactions are due solely to the rotational component of combined rotational and translational motion. We conclude that the perception of rotational motion relies on form–motion interactions that are independent of the processing underlying translational motion.

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1. Introduction

As we observe an object moving through the world, does our visual system independently process the rotational and translational components of its motion or not? It is an open question whether – and if so, how – translational and rotational motion computations interact. Motion perception is often studied using stimuli that either translate or rotate, but rarely do stimuli simultaneously rotate and translate in a single experiment. While segregating these motion components permits the isolation of perceptual mechanisms underlying each type of motion, this common psychophysical approach is not ecologically valid. Consider the motion of a tiger, for example. It will have a clear translational component as the animal leaps from point A to point B, but at the same time the body of the animal is likely to twist, turn and change orientation relative to the ground. Given that objects can and typically do translate and rotate as they move, under normal circumstances the visual system must process both translation and rotation simultaneously. Here we explore the interaction between these two types of motion by considering simple geometric stimuli that translate and rotate simultaneously.

Several motion processing models can be proposed for how translation and rotation processes may interact. At one extreme, it could be that both types of motion processing are reducible to a single type of processing, such as the serial analysis of local

motion energy. At the other extreme, it could be that translational and rotational motion are processed by entirely different systems, with different sets of primitive translational and rotational motion energy detectors. Between these two extremes lie many possibilities where certain aspects of translational and rotational motion processing are shared, whereas others are specialized for the particular problems posed by each.

Motion perception as a whole is fundamentally constrained by the fact that motion-sensitive neurons in early visual cortex have small receptive fields and only have access to a small area of the visual field. Because of this so-called 'aperture problem' multiple types of global motion can lead to identical local motion information. This makes it impossible for an individual motion-tuned neuron in, say, V1 or V2, to identify the true velocity of a moving object (Adelson & Movshon, 1982; Fennema & Thompson, 1979; Marr, 1982; Nakayama & Silverman, 1988a, 1988b). It is widely held that the perception of an object's motion, and of a rotating object in particular, is constructed on the basis of spatial integration of local translational motion estimates (Grzywacz & Yuille, 1991; Hildreth, 1984, 1990; Horn & Schunck, 1981; Nakayama & Silverman, 1988a, 1988b; Weiss & Adelson, 2000; Weiss, Simoncelli, & Adelson, 2002). In computer vision, it has been proposed that several constraints (e.g. rigidity, smoothness) within the motion computation system, allow the computation of a single motion estimate that is consistent with all local measurements, with any combination of translational, rotational and deformational motion (Hildreth & Ullman, 1982; Poggio, Torre, & Koch, 1985; Weiss & Adelson, 1998).

The major projection from primary visual cortex to MT plays an important role in computing translational motion trajectories

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(Majaj, Carandini, & Movshon, 2007; Rust et al., 2006). However, less is known about how complex object-motions such as rotation or expansion are processed. Neurons tuned to particular optical flow patterns, such as full-field expansion, contraction, translation, spiral motion or rotation, have been found, particularly in dorsal MST (MSTd; Graziano, Andersen, & Snowden, 1994; Tanaka, 1998; Tanaka & Saito, 1989; see also Burr, Badcock, & Ross, 2001; Snowden & Milne, 1996). Such full-field motion detectors in MSTd are thought to arise by taking input from lower-level units tuned only to local translational motion energy (Morrone, Burr, & Vaina, 1995; Saito et al., 1986; Simoncelli & Heeger, 1998; Tanaka, Fukada, & Saito, 1989). However, optic-flow motion patterns most commonly arise due to the motion of the observer rather than the motion of objects in the environment (Lee, 1980). While observer-generated motion signals must be accounted for in order to accurately perceive the motion of an object (Gibson, 1966), in this paper we primarily concern ourselves with the motion of objects in the absence of observer-generated full-field motion (i.e., a stationary observer). In contrast to self-generated optic flow, object motion is rarely full field, and is typically confined to the boundaries of the object itself.

When an object translates and rotates simultaneously, a distinct challenge arises in determining how much of the locally detected translational motion signal is generated by object translation and how much is generated by the rotation of the object. Is rotational object motion computed by integrating locally generated translational motion signals (in the same manner as full-field optic flow fields) or do the computations of translational and rotational object motions rely in part upon distinct and independent sources of information?

The independent processing hypothesis is supported by the fact that there are fundamental differences between translational and rotational motion that lead to distinct computational challenges. For example, because all points on a non-rotating, rigid contour translate with the same speed and direction as the whole object, the magnitude of any locally detected motion signal will be proportional to the actual translational speed of the object (Adelson & Movshon, 1982). For rotation, however, the angular velocity of a point on a contour is a function of its distance from the center of rotation, which is information that is not available locally; computing the center of rotation requires comparison of many locally measured motion signals across the image. As such, the perception of rotational motion likely relies upon processes that are at least in part distinct from the processes that underlie the perception of translational motion.

One possibility is that the visual system decomposes input into translational and rotational components at an early stage. But if so, how might this occur? Mathematically, the 2D rigid motion of an object can be decomposed into a combination of translation and rotation about the center of the object.[2] We have previously shown that objects defined by contours containing regions of high curvature are perceived to rotate around their centers faster than objects defined by contours that do not contain such regions (Caplovitz, Hsieh, & Tse, 2006; Caplovitz & Tse, 2007a, 2007b). One hypothesis for why this occurs is that high-curvature regions give rise to additional form-based motion signals that are stronger than those generated by low-curvature regions (Caplovitz, Hsieh, & Tse, 2006; Caplovitz & Tse, 2007a, 2007b; Hsieh & Tse, 2007). In addition, it has been demonstrated that translational motion in the direction of an elongated object's principal orientation is more readily perceived than motion orthogonal to it (Krolik, 1934; Metzger, 1936); Furthermore, elongated objects appear to translate faster when moving parallel

with rather than perpendicular to their orientation, and the magnitude of this effect increases with increasing elongation (Georges et al., 2002; Seriès et al., 2002). Here we used these two distinct form-induced speed illusions to investigate interactions between translational and rotational motion and form.

As the aspect ratio of an ellipse increases (becoming more elongated), the regions of contour located at the ends of the major axis become more highly curved for a given length major axis. We report here that when an ellipse both translates and rotates simultaneously, the relationship between contour-curvature and perceived velocity is dictated by the rotational component of motion in a fashion that is independent of the speed of the translational component of motion. In addition we report effects of elongation on perceived speed similar to those observed with strictly translational motion even when a rotational component is added to the motion trajectory. These results suggest that the processes underlying the perception of translational and rotational motion are mediated by analyses of form information that are largely independent in their effects on perceived motion.

2. General methods

2.1. Participants

Each person who participated in the experiments had normal or corrected-to-normal vision. Prior to the experiments, all participants included in this study gave written informed consent, according to the guidelines of the Department of Psychological and Brain Sciences and the internal review board of Dartmouth College. Naïve participants received $5 for each of the experimental sessions they completed. Five people (two naïve Dartmouth students and three authors) participated in Experiment 1, six people (all naïve Dartmouth students) participated in Experiment 2 and seven people (six naïve Dartmouth students and one author) participated in Experiment 3.

2.2. Stimulus presentation

The visual stimulator was a 2 GHz Dell workstation running Windows 2000. The stimuli were presented on a 23-in. SONY CRT monitor with 1600×1200 pixels resolution and 85 Hz frame rate. Luminance values were measured using a Spectra® Spotometer® (Photo Research, Chatsworth, CA, USA) at a distance of 18 cm. Participants viewed the stimuli on a black background (0.55 cd/m^2) from a distance of 76.2 cm with their chin in a chin rest. Participants were required to maintain fixation on a small yellow square (93.88 cd/m^2) fixation spot that subtended $0.05°$ of visual angle. Fixation was ensured using a head-mounted eyetracker (Eyelink2, SR research, Ontario, Canada; Tse, Sheinberg, & Logothetis, 2002). Any time the subject's monitored left eye was outside a fixation window of $1.5°$ radius, the trial was automatically aborted, and a new trial was randomly selected from those remaining. The eyetracker was recalibrated whenever the subject's monitored eye remained for whatever reason outside the fixation window while the subject reported maintaining fixation. Once calibration was completed, the experiment resumed with a random trial.

2.3. Terminology

In the experiments described here, the stimuli either translate along circular trajectories (Fig. 1) and/or rotate about their centers (i.e., Fig. 3). When saying 'translate along a circular trajectory' we draw an explicit distinction with the motion of an object that is rotating about its center. The two forms of motion are distinct from each other in one fundamental way. As an object translates along a

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[2] In fact there are an infinite number of possible decompositions that arise because the object could in theory rotate about any point in space, not just its center (Goldstein, 1979; Yang, Shimpi, & Purves, 2002).
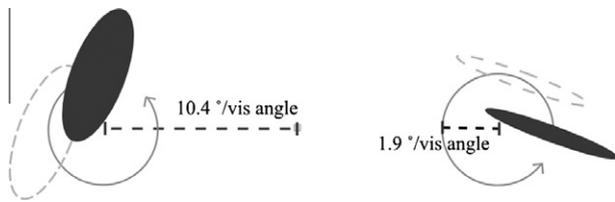
Fig. 1. The stimulus configuration used for Experiment 1. Each ellipse translated along a circular trajectory; however, the orientation of each ellipse never changed relative to the world. Note that the colors are changed here for presentation purposes; in the experiment, the ellipses were white and the background was black.

circular trajectory, although it is changing its angular position relative to the center of the trajectory, at any one moment in time the velocities of all points along the object's contour are in fact the same and therefore do not depend upon a point of origin. In contrast, as an object rotates around its center, the velocities of all points along the contour are all different and critically depend upon the center of rotation. For clarity, it is important to dissociate the angular velocity as the stimuli traverse circular trajectories, from the angular velocity with which the stimuli rotate about their centers. Additional confusion can arise because it is common to describe the speeds of visual stimuli in terms of degrees of visual angle per second. To avoid confusion, we use the term 'orbital speed' to describe the angular speed with which a stimulus traverses along a circular trajectory and 'rotational speed' to describe the angular speed with which it rotates about its center. In both cases, we use units of 'degrees of radius per second' to distinguish these velocities from units of degrees of visual angle per second.

3. Experiment 1: aspect ratio and perceived translational speed

This experiment was designed to investigate the potential independence of translational and rotational motion processing. The stimuli used were solid ellipses of various aspect ratios. Ellipses translated along a circular orbital path, but did not change their orientation relative to their centers.

3.1. Procedure

In each trial, participants were presented with two white (39.81 cd/m^2) translating ellipses on a black (0.55 cd/m^2) background for 500 ms. Ellipses translated along two circular trajecto-

Fig. 3. The stimulus configurations used for Experiment 2. (A) The "race car" stimulus configuration, where the ellipses have a point-leading edge of rotation. (B) The "clockhand" stimulus configuration, where ellipses have a flat-leading edge. Unlike the case in Experiment 1, here the ellipses also rotate about their centers. Note that the colors are changed here for presentation purposes; in the experiment, the ellipses were white and the background was black.

ries, each centered on a point ±10.4° visual angle along the horizontal axis away from the central fixation spot with a radius from the center point to the center of the ellipse of 1.9° of visual angle (Fig. 1). Participants were required to indicate by pressing one of two buttons in a two alternative forced choice design (2AFC) which of the two ellipses moved faster; the one to the left or the one to the right of fixation. On every trial, one ellipse (standard) had the same aspect ratio (AR = 1.86; 8.2° × 4.4° of visual angle, height × width) and same orbit speed (364° of radius per second around the center of the orbital path or 12.07° of visual angle per second). The other (test) ellipse had the same major axis as the standard and an aspect ratio of 1.86, 2.56, 3.90 or 8.75. Test ellipses with the same aspect ratio (1.86) as the standard were used as a control condition to verify the efficacy of the 2AFC procedure and participants' ability to accurately report their perceived speeds. On a given trial, the test ellipse had an orbit speed selected from the following list: 91°, 182°, 227.5°, 273°, 318.5°, 364°, 409.5°,

Fig. 2. Results from Experiment 1. The psychometric response functions, plotted for the mean responses to the four different ellipse aspect ratios, are illustrated on the left side of the figure, along with examples of the four different aspect ratios. The means of each subject's points of subjective equality for each of the aspect ratios are illustrated on the right. For reference, the shading of the boxes surrounding each of the ellipses corresponds to the shading of the curves and bars; the same is true in subsequent figures. A very small effect of aspect ratio on perceived speed is observed.

455°, 500.5°, 546°, 637° of radius per second or, respectively, 3.02°, 6.04°, 7.54°, 9.05°, 10.56°, 12.07°, 13.58°, 15.09°, 16.60°, 18.11°, 21.12° of visual angle per second. The direction of movement along the trajectory (clockwise or counterclockwise) was randomly and independently determined on each trial, so that the two ellipses could either move in the same or opposite directions. In addition, the orientation, starting location along the circular trajectory and side of presentation of each ellipse was randomly determined independently for each ellipse on every trial. Trial types were pseudo-randomly presented so that during an entire session, 10 trials of each aspect ratio and speed pairing were presented for a total of 440 trials. Each subject completed three individual sessions.

3.2. Results

The percentage of times that the test ellipse was perceived to move faster than the standard ellipse was computed. Thus, for each of the four test ellipses, eleven values (one for each orbit speed) were calculated. The following function was then fit to the corresponding data for each aspect ratio using MATLAB: $f(x) = 100 \times \left[\frac{e^{b_1+xb_2}}{1+e^{b_1+xb_2}} \right]$. The resulting curves, plotted for the mean responses across participants, are shown on the left side of Fig. 2. The clear and steep-sloped sigmoidal shaped psychometric curve derived from the "control" condition in which both control and test ellipses have the same aspect ratio confirm that participants were able to perform the task and accurately report their percepts.

The right side of Fig. 2 illustrates the point of subjective equality (the orbit speed at which each test ellipse needed to translate in order to be perceived as equal to the speed of the standard ellipse) for each of the four curves. These values were determined for each subject by interpolating the 50% chance level ($x = -b_1/b_2$; i.e., the point of subjective equality) from the function fit to the corresponding data. For presentation purposes these values were then averaged across participants. A repeated measures ANOVA revealed a significant main effect of aspect ratio on perceived translational speed ($F(3,12) = 4.008$, $p = 0.034$, $\eta_p^2 = 0.501$, where η_p^2 or 'partial eta squared' is a measure of effect size). However unlike what is observed for ellipses that rotate about their centers a follow-up polynomial contrast revealed no significant linear relationship between aspect ratio and perceived translational speed ($F(1,4) = 6.227$, $p = 0.067$, $\eta_p^2 = 0.609$). That is to say, increasing aspect ratio did not lead to a systematic increase in perceived speed.

Unlike the rotational motion stimuli we have previously studied that revealed a strong linear relationship between aspect ratio and perceived rotational speed, these data show that there is only a weak increase in perceived speed of an ellipse translating along a circular trajectory as a function of increasing aspect ratio. While the results of the ANOVA indicate that aspect ratio may influence (albeit the linear contrast was not significant at an alpha level of 0.05) perceived translational speed, the magnitude of this influence is dramatically less (i.e., the PSE$_{thin}$ is approximately 92% of PSE$_{fat}$ for the translational case) than previously observed for purely rotational motion (where PSE$_{thin}$ is approximately 55% of PSE$_{fat}$; Caplovitz, Hsieh, & Tse, 2006; Caplovitz & Tse, 2007a, 2007b). The most likely explanation of why aspect ratio influences perceived speed here is that it arises as a residual effect of direction of rotation relative to the axis of orientation rather than a more generalized effect; That is, as an ellipse orbits without rotating around its own center, its orientation will be tangent to the circular path twice during each orbit. At these orientations, skinnier ellipses should appear to translate faster than fatter ellipses (Georges et al., 2002; Seriès et al., 2002). When the orientations are orthogonal to the circular path, however, skinnier ellipses should appear to translate slower than fatter ellipses (Georges et al., 2002; Seriès et al., 2002). Thus in theory these effects should cancel each other

out, but in practice, small residual effects may be expected and could account for the non-systematic yet significant relationship between aspect ratio and perceived translational speed.

It should also be noted that because the stimuli were always presented for 500 ms the distance they travelled along the circular trajectories on any given trial can potentially serve as an additional cue to indicate which of the ellipses was moving faster. However, because we were not necessarily interested in perceived speed in absolute terms but rather in relative speed across aspect ratio, this potential confound is not of great concern in this or the following experiment.

4. Experiment 2: aspect ratio and perceived speed for combined translational and rotational motion

The goal of Experiment 2 was to further investigate the relationship between elongation, contour curvature and perceived speed. We examined motion trajectories that contain both translational and rotational motion (relative to the center of the ellipse). Here the trajectories were chosen such that the rotational and translational components were matched. Specifically, the rotational speed around the center of the ellipse was matched to the orbit speed of the center of the ellipse as it translated around similar circular trajectories as were used in Experiment 1. Thus, the time it took for the ellipse to complete one rotation around its own center was also the time needed to complete one path around the circular trajectory.

In addition, we investigated the effect of the ellipse's orientation relative to the path of translation on perceived speed. Specifically, two distinct stimulus configurations were presented, defined by the leading edge of rotation: either a 'point-leading edge' or a 'flat-leading edge' (see Fig. 3). The first case is analogous to a racecar driving along a circular path, and the second case is analogous to the second hand sweeping around the face of a clock. Importantly, the relative translational and rotational components are held constant between the two leading edge conditions. Therefore any differences in perceived speed between the leading edge conditions cannot be caused by differences in main effects of either rotation or translation among those conditions. Instead such differences must be due to an interaction between the form of the ellipse and its translation, rotation or both.

4.1. Procedure

The same general procedure as Experiment 1 was used for this experiment. Here, each ellipse translated along a circular path with a radius of 3.55° of visual angle (slightly larger than in Experiment 1) centered ±10.4° of visual angle from fixation, while it simultaneously rotated about its own center. The standard ellipse had an aspect ratio of 1.85, but was slightly smaller than in Experiment 1 (6.1 × 3.3° of visual angle), and on each trial had matched orbit and rotational speeds of 101.64° of radius per second corresponding to 6.30° of visual angle per second. Each test ellipse had a major axis that also subtended 6.1° of visual angle and had an aspect ratio selected from 1.85, 2.54, 3.8 or 8.13. On each trial the test ellipse had a matched orbit and rotational speed selected from the following list: 18.48°, 36.96°, 55.44°, 73.92°, 92.4°, 101.64°, 110.88°, 129.36°, 147.84°, 166.32°, or 184.8° of radius per second around the circular trajectory or, equivalently, 1.14°, 2.29°, 3.43°, 4.58°, 5.72°, 6.30°, 6.87°, 8.01°, 9.16°, 10.30°, or 11.45° of visual angle per second. The orientations of both the test and standard ellipses were chosen so that on half the trials the leading edge of motion was within ±15° of radius of the point of maximal contour curvature (point-leading edge) and on the other half, within ±15° of radius of the point of minimal contour curvature (flat-leading edge).

This orientation jitter was used to prevent participants from employing orientation specific strategies for deriving their responses.

On any given trial, the two ellipses were presented for 500 ms and were always from the same leading edge group. The direction of rotation of each was randomly selected to be clockwise or counterclockwise. As in Experiment 1, the starting locations along the corresponding trajectories were randomly determined for each ellipse independently on each trial, as were the sides on which the standard and test ellipses were presented. Participants were required to make a 2AFC judgment of velocity by pressing one of two buttons to indicate which of the two ellipses had a greater speed. Specifically, participants were instructed to indicate which of the two ellipses appeared to be moving faster. No explicit instructions regarding rotational or translational motion were given. Trial types were pseudo-randomly presented so that for each of the two leading edge conditions, each aspect-ratio and speed pairing was presented 5 times, for a total of 440 trials per session. Each subject performed 4 of these sessions.

4.2. Results

The data from both the point-leading edge (Fig. 4A) and flat-leading edge (Fig. 4B) conditions indicate that perceived speed under conditions of combined rotational and translational motion increases as a function of aspect ratio. A 2×4 repeated measures ANOVA, with factors of leading edge and aspect ratio, was performed on the PSEs (Fig. 4). Importantly, this analysis revealed a significant main effect of aspect ratio ($F(3, 15) = 10.386$, $p = 0.001$, $\eta_p^2 = 0.675$). The follow-up linear contrast revealed a significant linear relationship between aspect ratio and perceived speed ($F(1, 5) = 13.124$, $p = 0.015$, $\eta_p^2 = 0.724$). In addition, the analysis revealed a main effect of leading edge ($F(1, 5) = 10.792$, $p = 0.022$, $\eta_p^2 = 0.683$). As can be seen in Fig. 4, the effect of aspect-ratio on perceived speed was greater for the point-leading edge than with the flat-leading edge. This observation was confirmed by a significant ($F(3, 15) = 3.607$, $p = 0.038$, $\eta_p^2 = 0.419$) interaction between leading edge and aspect ratio.

These results are consistent with the hypothesis that the motion trajectories are processed as though they contain both a translational and rotational component. As would be expected for rotational motion, in both leading edge conditions, the thinner ellipses were perceived to move faster than the fatter ellipses.
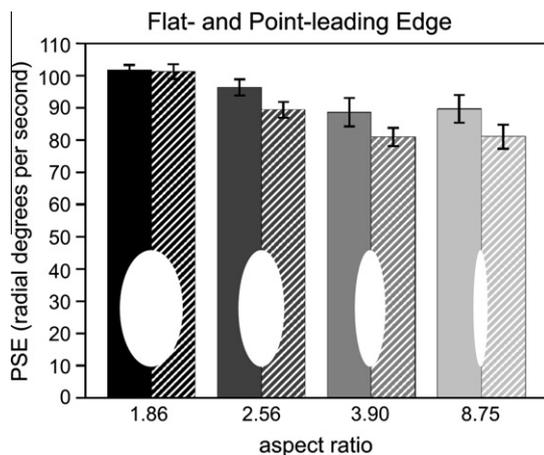
However, the effect was smaller in the flat-leading edge condition. This is to be expected if the form-contributions to translational and rotational motion arise through independent and additive mechanisms: It has been shown that elongation will have a facilitatory effect on perceived speed when the orientation is parallel to the direction of translation, and an inhibitory effect when perpendicular to the path of translation (Georges et al., 2002). If the influence of form on perceived speed were strictly due to the translational component of the trajectory, then in the flat leading edge configuration, one would expect fatter ellipses, which produce weaker inhibitory effects (Georges et al., 2002), to appear to move faster than thinner ones, which produce stronger inhibitory effects (Georges et al., 2002). Instead, our results suggest that form influences translational and rotational motion independently.

5. Experiment 3: varying translational speed

Having established that motion trajectories get decomposed into translational and rotational components, each subject to its own interaction with an object's form, the goal of this experiment was to determine whether these distinct types of motion mutually influence one another. In this experiment we varied the speed of translation relative to the speed of rotation and examined the resultant effect of aspect ratio on perceived speed. Instead of ellipses 'orbiting' along a circular trajectory, here we had each ellipse translate vertically while simultaneously rotating around its own center (see Fig. 5). We decided to use a linear trajectory because illusory acceleration and deceleration were observed when the duration needed by an ellipse to complete one full rotation and one full circular orbit was not matched.

5.1. Methods

5.1.1. Procedure

The same general procedure was used as in Experiments 1 and 2. On any given trial, both the standard and test ellipses translated vertically (see Fig. 5) at the same speed selected from the following list: (4°, 11.8°, 18.8° of visual angle per second) and were presented for 500 ms. The standard ellipse always had the same aspect ratio 1.85 (6.1° × 3.3° of visual angle) and rotational speed (136.59° of radius per second). The aspect ratio of the test ellipse was selected from the following list: (1.85, 2.54, 3.8) and had a rotational speed selected from one of seven possibilities: 9.11°, 113.83°, 127.48°, 136.59°, 145.7°, 159.36°, 264.07° of radius per second. The direction of translation (up or down) was the same for both the test and standard ellipses, but their common direction was randomly determined for each trial. The vertical start- and end-points of each translational velocity condition were selected such that the visible path of the stimuli was centered with regard to fixation. On each

Fig. 4. Results of Experiment 2. The figure shows the means of participants' points of subjective equality, for each aspect ratio. Results from the flat-leading edge stimulus configuration are shown with filled bars, whereas results from the point-leading edge configuration are shown with hatched bars. A smaller influence of form on perceived speed is observed in the flat-leading edge condition.

Fig. 5. The stimulus configuration used for Experiment 3. Here the ellipses translate in the vertical axis while simultaneously rotating about their centers. Note that the colors are changed here for presentation purposes; in the experiment, the ellipses were white and the background was black.

trial, the initial orientation of each ellipse was randomized independently. Both ellipses had the same direction of rotation, but this direction was randomly determined on each trial. The sides on which the test and standard ellipses were presented were randomly determined on each trial. The translational speeds as well as the aspect ratio and rotational speed of the test ellipses were pseudo-randomly determined across trials. Overall, 10 trials of each condition were presented in a session for a total of 630 trials. Each subject performed one session.

Participants were required to make a 2AFC judgment of velocity by pressing one of two buttons to indicate which of the two ellipses had a greater speed. Specifically, participants were instructed to indicate which of the two ellipses appeared to be moving faster. As in Experiment 2, no explicit instructions regarding rotational or translational motion were given.

5.2. Results

The data from Experiment 3 indicate that translational speed did not interact with the influence of aspect ratio on perceived speed. Specifically, the points of subjective equality for each aspect ratio across the three translational speeds were nearly identical (see Fig. 6), indicating that across translational speeds, each test ellipse needed to rotate at a similar angular velocity in order to be perceived as having the same speed as the standard. A two way ANOVA with factors of aspect ratio and translational speed confirmed a main effect of aspect ratio: $F(2, 12) = 63.350$, $p < 0.001$, $\eta_p^2 = 0.913$. The follow-up linear contrast revealed a significant linear relationship between aspect ratio and perceived speed ($F(1, 6) = 89.364$, $p < 0.001$, $\eta_p^2 = 0.937$). In contrast, there was no significant main effect of translational speed: $F(2, 12) = 0.450$, $p = 0.648$, $\eta_p^2 = 0.070$. Importantly, there was no significant interaction between translational speed and aspect ratio: $F(4, 24) = 0.712$, $p = 0.592$, $\eta_p^2 = 0.106$. This demonstrates that the relationship between perceived speed and aspect ratio is independent of the speed at which the ellipses translate.

One potential confound in Experiment 3 is that ellipses in fast translation conditions traversed a longer and therefore more peripheral path than the ellipses in slow translation conditions. There are well-known asymmetries in the perception of motion between foveal and peripheral vision (Levi, Klein, & Aitsebaomo, 1984; McKee & Nakayama, 1984; Shapiro, Knight, & Lu, 2011; Shapiro, Lu, Huang, Knight, & Ennis, 2010; Tse & Hsieh 2006). These asymmetries may obscure influences of translational speed. For example, it is possible the influence of form is in fact reduced with increased translational speed, but that this is counteracted by an 'increased' influence of form when stimuli are viewed in the periphery or visa-versa. To address this potential confound we conducted two additional control experiments which investigated effects of eccentricity. The results of these control experiments can be found in Supplementary materials. They indicated that this potential confound is unlikely to account for the observed results.

6. General discussion

In the experiments reported here, we sought to investigate the perceptual interactions between translational and rotational motion. In particular, we examined the relationship between the form of an object and the speed with which it is perceived to move in the context of combined translational and rotational motion. The experiments reported here had four main results:

(1) Unlike the large effect size observed in the case of rotational motion, there is little or no influence of an object's form on the net speed that it is perceived to translate along a circular orbit in the absence of rotation around its own center.
(2) When an ellipse also rotates about its center as it translates, the form of the ellipse greatly influences its perceived speed. Namely, a 'skinny' ellipse that is both translating and rotating will appear to move faster than a lower aspect ratio 'fat' ellipse that is translating and rotating along the same orbit and with the same rotational speed.
(3) When the ellipse was oriented so that a region of high curvature served as the leading edge as it translated and rotated along it trajectory (i.e., like a car driving along a circular track), we observed a greater influence of form on perceived speed than when the ellipse was oriented so that a region of low curvature served as the leading edge (i.e., like the movement of a clockhand). This effect arises due to an interaction of the shape/orientation of the ellipses and translational motion and reveals an additive relationship between form's influences on translational and rotational motion.
(4) The degree to which the contour curvature of the ellipse influenced its perceived speed of motion was largely unaffected by the speed at which the ellipse translated while simultaneously rotating.

6.1. Implications of results

Taken together, the results of the experiments presented here indicate two distinct interactions between an object's form and its perceived speed. In the case of translation without rotation, the elongation of an object and its orientation relative to the direction of motion influences how fast it is perceived to translate (Georges et al., 2002; Seriès et al., 2002). In the case of rotation without translation, the sharpness of contour curvature influences
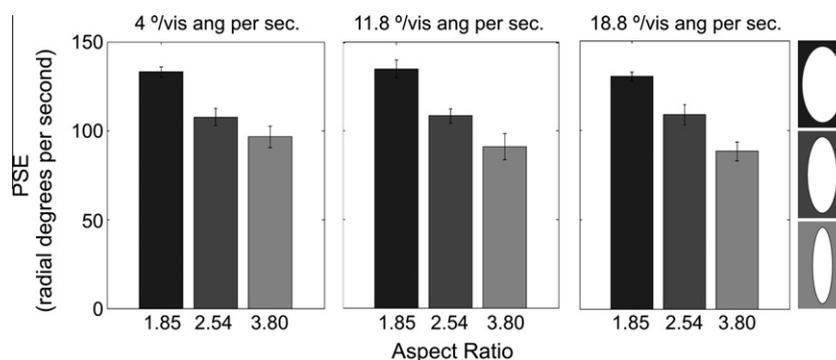
Fig. 6. Results of Experiment 3. The figure shows the point of subjective equality for each test ellipse aspect ratio, i.e., the angular velocity (in radial degrees per second) at which the test ellipse had the same perceived speed as the standard ellipse, plotted for each of the three translational speeds. Increasing the speed at which the ellipses translated had little effect on the influence of form on perceived speed. The three test ellipse aspect ratios are illustrated on the right side of the figure.

how fast an object appears to rotate (Caplovitz & Tse, 2007a, 2007b; Caplovitz, Hsieh, & Tse, 2006). Importantly, when an object is both translating and rotating about its center, these form–motion interactions appear to be independent of each other and manifest themselves additively in the overall perception of object speed. Specifically, the presence of rotation does not appear to influence the effects of form on translation (Experiment 2), and the presence of translation does not seem to greatly influence the effects of form on rotation (Experiments 2 and 3).

These experiments reveal a fundamental difference between the perception of translational and rotational motions. In particular, the form of a rotating object leads to illusory speed percepts that are not perceived if the object is translating without rotating. Why might this be? One hypothesis is that unlike translational motion, the rotational motion of an object poses three distinct computational challenges that the visual system must overcome in order to produce an accurate motion percept. (1) First, unlike the case for translation of a rigid object, where all portions of the contour in fact move with the same velocity, as an object rotates, each portion of its contour moves with a different local velocity. (2) Second, in many instances, the motion of a rigidly rotating object (particularly those defined by a smooth, continuous and closed contour) can be equally consistent with the motion of an object that is continuously deforming in shape (Wallach, Weisz, & Adams, 1956; Weiss & Adelson, 2000). (3) Third, angular velocity can only be computed for a given moving point on a contour relative to the center of its rotation. However, the center of rotation is typically far away from the motion that is measured at a point. Moreover, the center of rotation may itself carry no motion signal. Whereas local motion measurements arising along certain points on a contour, such as corners or terminators, are sufficient to recover the direction of translation of an entire rigid object (Wallach, 1935) this is not the case for rotational motion. Because of the need to localize a center of rotation, rotational motion requires a global analysis of all (or at least a distributed sampling of) locally measured motions in order to determine the angular velocity of a rigidly rotating object. It is possible that an analysis of an object's form may facilitate the identification of the center of rotation.

The results presented here are consistent with the hypothesis that complex object motions are decomposed at each instant, such that a rotational component is computed relative to the center of the object, and not relative to any other point that could serve as a center of rotation. This means that the center of an object is explicitly computed before angular velocity can be computed relative to that point. Together, the three computational challenges described above place constraints on the processing of rotational motion that do not arise for translational motion. Because the computational problems posed by translational and rotational motion differ, it is likely that the neuronal processes underlying the perception of rotational object motion recruit sources of information that can resolve these challenges that are not needed in the processing of translational motion.

The effect of elongation and translational motion is thought to arise from a local interaction between the processing of an object's orientation and the direction of translational motion (Georges et al., 2002; Seriès et al., 2002). This is in distinct contrast to the global analysis of form hypothesized to underlie the processing of rotational motion. The additive effects of the two form–motion interactions observed in Experiment 2 are consistent with the hypothesis that they arise in a serial manner. Specifically, the local influences of elongation on translational motion arise prior to the stages of global form analyses that contribute to the processing of rotational motion.

One hypothesis for why form-induced motion illusions arise at all, particularly in the case of rotational motion, is based on the fact that regions of high contour curvature and contour curvature discontinuity such as corners, junctions and terminators move unambiguously; They provide information that can solve the aperture problem and indicate the velocity of an object, given that certain reasonable assumptions, such as object rigidity, are met (Ullman, 1979). As such, if the visual system can identify such contour features as belonging to the rotating object, they may serve as 'trackable features' whose unambiguous motion can be selectively used to compute angular velocity and be attributed to the object as a whole. According to this hypothesis, regions with high contour curvature represent trackable features that provide either stronger motion signals or more accurate motion estimates than 'poorly-trackable' regions with low contour curvature, thereby leading to the illusory differences we observe in perceived angular velocity. In past work, we demonstrated that not only are skinny ellipses (with high contour curvature) perceived to rotate faster than fatter ellipses (with low contour curvature) rotating in fact at the same objective angular velocity, but a similar effect is also observed in objects with different shapes as well. Specifically, a rectangle that has had its corners replaced by uniformly curved regions of contour (rendering them less trackable) will appear to rotate more slowly than a regular rectangle. Furthermore, the degree of slowdown is parametrically modulated by degree of curvature of the replaced corners (Caplovitz, Hsieh, & Tse, 2006).

However, in the case of rotation, the motion of such trackable features is subject to the same limitation of needing the establishment of a center of rotation. As salient form cues, regions of high curvature are particularly informative for establishing an object's contour (Attneave, 1954) and in addition, regions of high curvature can serve an important role in disambiguating rigid-rotational motion from non-rigid deformations (Ullman, 1979; Wallach, 1976; Wallach & O'Connell, 1953). Establishing both an object's contour and object rigidity may contribute towards the identification of the center of rotation. Taken together, the identification and processing of form-defined trackable features can provide essential information that can be used to overcome the challenges facing the visual system in constructing percepts of rotational motion.

6.2. Component motion

A non-mutually exclusive alternative hypothesis for why the aspect ratio of an ellipse should influence its perceived angular velocity is based on the integration of locally detected motion signals. In particular, the form of an object will in part determine the relative magnitudes of the locally detected motion signals arising along its contour. As such, the form of an object directly influences the inputs that are potentially available for global motion-integration processes, like those proposed by many models of motion perception (Adelson & Movshon, 1982; Bowns, 2001, 2002; Hildreth, 1984; Lu & Sperling, 1995; Rust et al., 2006; Weiss & Adelson, 2000; Yo & Wilson, 1992). Indeed, we found that in general the magnitude of local motion signals (and the maximum in particular) computed along an object's contour co-varied both with contour curvature and the speed at which the object was perceived to rotate (Caplovitz, Hsieh, & Tse, 2006). It is possible therefore that, in some instances, the integration of locally detected motion signals that arise along the contour of an object with high curvature leads to increased perceived angular velocity compared to objects with low-curvature contours.

The stimuli and results of the experiments presented here allow us to again look at the relationship between the magnitudes of local motion signals measured along a contour and perceived speed. For a given motion trajectory, we computed the local motion signals that would be expected to arise along the elliptical contours (see Fig. 7). This was done by computing the normal-projection relative to the contour of the velocity vector at each contour location. This normal component of the velocity vector is commonly
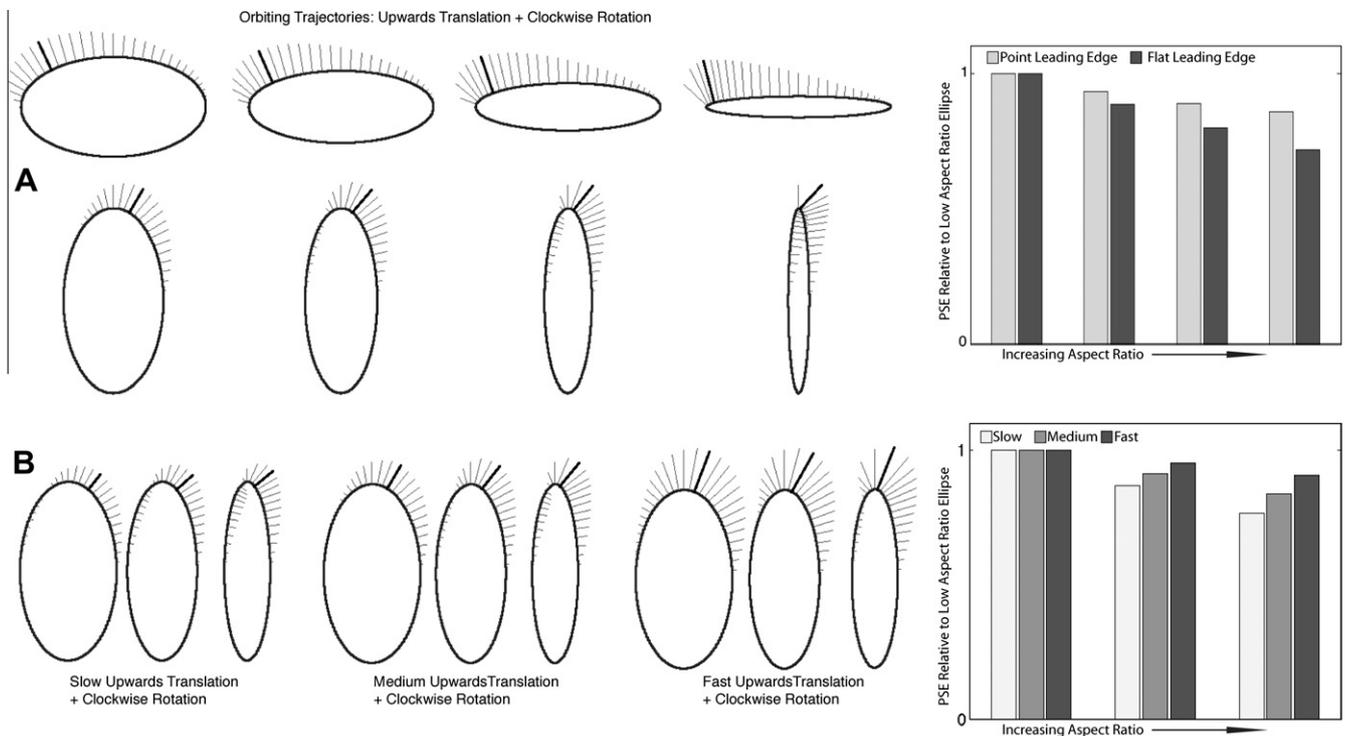
Fig. 7. Modeling component motion vectors. Local motion signals expected to arise along elliptical contours, based on the component vector at each contour location. In each case, the bold-faced vector indicates the component with the largest magnitude. On the right side of the figure, the expected relative local motion magnitudes are plotted as PSEs relative to the speed of a low aspect ratio ellipse. The PSE values are computed on the basis of the corresponding vectors with the maximum magnitude. (A) The component vectors in both the point- and flat-leading edge configurations such as those used in Experiment 2 are shown. Here, the component vectors incorrectly predict a larger speed illusion in the flat-leading edge than in the point-leading edge conditions. (B) Component motion at different translational speeds for configurations such as those used in Experiment 3. Here, the component vectors predict that the speed illusion should decrease in strength the faster an ellipse translates.

referred to as the 'component vector' and represents the locally-detectable motion signal derived from a motion-sensitive neuron subject to the aperture problem (Adelson & Movshon, 1982).

In the case of the purely translational motion of Experiment 1, we find that in general the magnitudes of the component vectors derived along the contour are relatively constant across aspect ratio. In particular, the maximum component vectors across aspect ratio are in fact constant and equal to the velocity of translation. This is due to the fact that there will always be a portion of an elliptical contour (of any aspect ratio and any orientation) that is locally orthogonal to the direction of motion and as such the component vector at that location will equal the translational velocity of the entire object. Thus, a very simple algorithm of finding the maximum motion vector along a contour does a good job of predicting the perceived speed of purely translational motion. It should be noted that this is a somewhat trivial result and many if not all existing motion-integration models (e.g., intersection of constraints, Adelson & Movshon, 1982; Nakayama & Silverman, 1988a, 1988b) will also arrive at this same result.

However, the magnitudes of the component vectors are not entirely consistent with the results of Experiment 2. On the one hand, consistent with our previously reported results, we again see a parametric relationship between the local motion signal magnitudes and contour curvature (and thus perceived speed) in both leading edge conditions (Fig. 7A). On the other hand, however, we find that the relative local motion magnitude between the high and low aspect ratio ellipses is greater for the flat-leading rather than point-leading edge conditions. This is in direct conflict with the results of Experiment 2 that show a great influence of aspect ratio in the point-leading edge condition. This lends further support to the conclusion that the leading-edge interaction arises due to an interaction between the object's shape/orientation and translational motion as described by Georges et al. (2002).

A further dissociation between perceived speed and the magnitudes of the local motion signals is observed for the configurations of Experiment 3. Here we find that the relative magnitudes of the component vectors between high and low aspect ratio ellipses decreases as the translational speed of the ellipses increases (Fig. 7B). However, we found no influence of translational speed in Experiment 3. Together, these results suggest that the perceived speed of objects that are simultaneously translating and rotating, and thus object motion in general, is not easily predicted by the magnitudes of the locally detected motion signals. This again suggests that in constructing the percept of rotational motion, the visual system recruits information that is presumably derived from an analysis of form that is not explicitly represented in the local motion signals present in the image.

6.3. Form motion interactions in the brain

The present work adds to at least a decade of emerging evidence that motion processing is influenced and constrained by global form processing. Global form analysis subserves motion processing in at least five important and related ways: (1) First, it permits figural segmentation dedicated to solving the problem of figure-to-figure matching over time that was revealed using transformational apparent motion as a probe (Hsieh, Caplovitz, & Tse, 2006; Tse, 2006; Tse & Caplovitz, 2006; Tse & Logothetis, 2002); (2) Second, form processing permits the definition of trackable features whose unambiguous motion signals can be generalized to ambiguously moving portions of an object to solve the aperture problem (Caplovitz, Hsieh, & Tse, 2006; Caplovitz & Tse, 2007a, 2007b); (3) Third, form processing permits the generation of emergent motion signals, for example, of virtual contours, that appear to underlie the conscious experience of motion (Caplovitz & Tse, 2006, 2007b; Hsieh & Tse, 2007; Kohler et al., 2010; Kohler, Caplovitz,

& Tse, 2009); (4) Fourth, form processing permits the influence of internal models of how forms are expected to move in disambiguating ambiguous motion signals, as occurs with biological motion (e.g. Johansson, 1973; Neri, Morrone, & Burr, 1999; Shiffrar & Freyd, 1990); and, finally, (5) Fifth, motion streaks appear to provide form-based information about motion direction (Apthorp, Cass, & Alais, 2011; Edwards & Crane, 2007; Geisler, 1999; Niehorster, Cheng, & Li, 2010).

Because the form analyses that subserve motion processing are diverse in their functions, it is not surprising that they are realized in multiple cortical areas. The process of segmentation based on contour cues described under (1) above is primarily a ventral process involving the lateral occipital complex (LOC) and also retinotopic areas such as V2 and V4, and perhaps even V1 (Tse, 2006; Tse & Caplovitz, 2006). In contrast, the form analyses involved in specifying trackable features described in (2) above may primarily be a dorsal process involving V3A, with potential involvement of the LOC and hMT+ (Caplovitz & Tse, 2007b; Tse & Caplovitz, 2006). It is not yet clear where (3), the generation of virtual contours and their motion signals, arises; fMRI and electrophysiological studies that have examined how contours are integrated into global shapes reveal that contour integration activates V1 and V2 in humans and monkeys (Altmann, Bulthoff, & Kourtzi, 2003; Gilbert & Wiesel, 1979, 1983, 1989; Kourtzi, Erb et al., 2003; Kourtzi, Tolias et al., 2003; Li, Piëch, & Gilbert, 2008; Rockland, Lund, & Humphrey,1982; Schmidt et al., 1997; Stettler et al., 2002; von der Heydt, Peterhans, & Baumgartner, 1984), but produces strongest activation in the LOC (Altmann, Bulthoff, & Kourtzi, 2003; Kourtzi, Erb et al., 2003). It is quite possible that some of the same mechanisms that underlie this type of contour formation also underlie the influence of elongation on translational motion (Georges et al., 2002; Seriès et al., 2002). Biological motion processing (4) appears to recruit circuitry in the superior temporal sulcus and elsewhere (e.g. Grossman & Blake, 2002). The analysis of form that underlies (5) motion streaks used as a cue for determining motion direction may take place in V1–V3 (Clifford, Mannion, & McDonald, 2009) as well as in other areas of the human motion processing complex, including the LOC and hMT+ (Krekelberg, Vatakis, & Kourtzi, 2005).

These results can be taken as further evidence for the inherently constructive nature of motion processing, and the importance of form operators in motion processing. While it is not clear where in the brain the analysis of form occurs that results in the perception of rotational motion, it likely occurs within some or all of the neural circuitry that realizes form–motion interactions described above. These results support the general thesis that there are, broadly speaking, two stages to motion perception: One, where motion energy is detected by cells in early visual areas tuned to motion magnitude and direction, and another stage where this detected information is operated upon by grouping and other visual operators that then construct the motion that will be perceived (Caplovitz & Tse, 2007a; Hsieh & Tse, 2007; Kohler et al., 2010; Kohler, Caplovitz, & Tse, 2009). This means that perceived motion, while constructed on the basis of locally detected motion information, is not itself detected or present in the stimulus.

7. Conclusion

An object's form influences its perceived speed. Specifically, in the context of rotational motion, an object's degree of contour curvature, directly contributes to perceived speed in a manner that does not occur for translational motion. It is likely that form information is used to overcome ambiguities that arise specifically when integrating local motion signals during object rotation,

leading to specific interactions between form and motion. The data reported here makes it clear that this rotational form–motion interaction is solely due to the rotational component of combined rotational and translational motions. The magnitude of this effect as demonstrated in Supplementary Experiment 1 is, moreover, unaffected by retinal location. From this, we conclude that the perception of rotational motion relies upon processes, in particular form–motion interactions that are in part independent of those underlying translational motion.

Acknowledgements

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.visres.2011.10.005.

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