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Vision Research 47 (2007) 1979–1991
Vision Research
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# Rotating dotted ellipses: Motion perception driven by grouped figural rather than local dot motion signals

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Received 15 May 2006; received in revised form 19 November 2006

**Abstract**

Unlike the motion of a continuous contour, the motion of a single dot is unambiguous and immune to the aperture problem. Here we exploit this fact to explore the conditions under which unambiguous local motion signals are used to drive global percepts of an ellipse undergoing rotation. In previous work, we have shown that a thin, high aspect ratio ellipse will appear to rotate faster than a lower aspect ratio ellipse even when the two in fact rotate at the same angular velocity [Caplovitz, G. P., Hsieh, P. -J., & Tse, P. U. (2006) Mechanisms underlying the perceived angular velocity of a rigidly rotating object. *Vision Research, 46*(18), 2877–2893]. In this study we examined the perceived speed of rotation of ellipses defined by a virtual contour made up of evenly spaced dots.

*Results:* Ellipses defined by closely spaced dots exhibit the speed illusion observed with continuous contours. That is, thin dotted ellipses appear to rotate faster than fat dotted ellipses when both rotate at the same angular velocity. This illusion is not observed if the dots defining the ellipse are spaced too widely apart. A control experiment ruled out low spatial frequency "blurring" as the source of the illusory percept.

*Conclusion:* Even in the presence of local motion signals that are immune to the aperture problem, the global percept of an ellipse undergoing rotation can be driven by potentially ambiguous motion signals arising from the non-local form of the grouped ellipse itself. Here motion perception is driven by emergent motion signals such as those of virtual contours constructed by grouping procedures. Neither these contours nor their emergent motion signals are present in the image.


*Keywords:* Local motion; Global motion; Rotational motion; Trackable features; Aperture problem; Contour curvature; Perceptual grouping

## 1. Introduction

How the visual system constructs the perception of motion from the temporal dynamics of the retinal image is a fundamental question that continues to challenge vision scientists. This is true even for the perception of relatively simple stimuli such as those completely defined by a closed contour. At the heart of the problem is the fact that an infinite number of 3D velocity fields can generate the same 2D retinal sequence. The local motion information at any point along a contour is consistent with an infinite number of possible motions that all lie on a 'constraint line' in velocity space (Adelson & Movshon, 1982). The problem of interpreting this many-to-one mapping is commonly termed the 'aperture problem' (Adelson & Movshon, 1982; Fennema & Thompson, 1979; Marr, 1982; Nakayama & Silverman, 1988a, 1988b).

Certain regions of a contour move unambiguously, and are not subject to the aperture problem. Such regions include corners, regions of high curvature, junctions, and terminators. It has been hypothesized that such 'trackable features' can be used to disambiguate ambiguous component motion signals that arise away from trackable features (Ullman, 1979). The motion of such trackable features themselves, however, is also ambiguous in the sense that

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0042-6989/$ - see front matter 
doi:10.1016/j.visres.2006.12.022

such contour features can arise, for example, through occlusion. The motion of such extrinsic (i.e. not comprising a part of the moving object) trackable features may not accurately represent the actual motion of the moving object (Nakayama & Silverman, 1988a, 1988b). In order to distinguish spurious motion signals arising from extrinsic trackable features from the informative motion signals arising from intrinsic trackable features, it would seem that the visual system must carry out a rapid global analysis of form, including an analysis of occlusion relationships, if it is to make use of trackable features as a cue to motion at all. In short, trackable features offer a powerful solution to the local ambiguity posed by the aperture problem. However, they give rise to a new ambiguity in interpreting local motion signals that can only be solved by a stage of global form analysis that specifies which motion signals arise intrinsically from a moving object. This would appear to involve, at a minimum, grouping procedures that can discount occlusion and link image cues into moving contours, surfaces, and objects. Recent work (Caplovitz & Tse, 2006a, 2006b; Tse, 2006; Tse & Logothetis, 2002) suggests that just such a stage of global form analysis precedes and influences motion perception.

Here we continue our efforts to specify the nature of these form-motion interactions by determining the types of motion signals that arise from dots that can be grouped into global forms. Unlike continuous contours or contour-defined trackable features, the motion of a single dot is in principle completely unambiguous and not subject to the aperture problem. In this paper, we investigate how the perception of the motion of a single dot is influenced by the presence of additional dots. For example, once multiple dots have been grouped into a contour, the motion of that virtual contour could suffer from the aperture problem. The central question addressed by this research is the following: Is the motion percept driven primarily by the unambiguous motion signals of individual moving dots in the image, or by the potentially ambiguous motion signals that would emerge after dots are grouped into contours?

We address this question by investigating the perceived rotational motion of illusory elliptical contours constructed through the configuration of multiple dots spaced equally along a smooth, virtual contour. Rotating ellipses exhibit a distinct illusory percept that we have previously characterized: there is a systematic relationship between the aspect ratio of an ellipse and the speed at which it is perceived to rotate (Caplovitz, Hsieh, & Tse, 2006). Specifically, a thin ellipse appears to rotate faster than a fatter ellipse spinning at the same actual angular velocity. We raised the hypothesis that the illusory percept results from the 'trackability' of the contour-defined trackable features, namely the regions of high positive curvature located at the ends of the ellipse. If the relative contour curvature is high (as is the case with a thin ellipse) then the region will be highly trackable and thus lead to a more accurate estimate of rotational speed. On the other hand, if the relative curvature is low (as is the case for a 'fat' ellipse) then the region will be poorly trackable and lead to a less accurate (slower) estimate of rotational speed. Furthermore, we questioned whether the illusory percept could be accounted for by the integration of ambiguous low-level motion signals.

In the present study, we use the presence (or lack thereof) of the speed illusion as an objective measure for how the motion percept of the rotating virtual elliptical contours is being constructed. In particular, if the speed illusion is observed, then we can conclude that the illusory percept is not arising from aperture-problem induced ambiguities in the low-level local motion signal (since there are no aperture-problem induced ambiguities for individual dot motion). In contrast, if the speed illusion is not observed, then we can conclude that the lack of aperture-problem induced ambiguities in the local motion signals is sufficient to allow for an accurate motion percept.

It is important to note that the perception of rotational motion is beset with an ambiguity that goes beyond that imposed by the aperture problem. Locally in the image, the only information available is the translational velocity at a given location in the visual field. However, for the perception of coherent rotational motion, an accurate computation of angular velocity at each point in the image must also take place. This computation must take into account not only the local translational velocity but also the distance from the center of rotation which is not explicit in the local motion signal, even for an individual dot, and which must be computed by the visual system before the angular velocity of a rotating figure can be determined. For example, a dot moving with a particular instantaneous translational velocity could in fact be rotating at any of an infinite number of angular velocities depending on its distance from the center of rotation. As such, if the illusory speed percept is observed among dotted ellipses, we must further identify whether the illusion arises solely from a failure to compute angular velocity directly from the local dot motion signals, or whether the motion percept is driven at least in part by motion signals generated after the construction of the virtual contour or after a stage of grouping that links the dots into a global shape. In this way we seek to identify and characterize the interactions of the ambiguous contour-motion and unambiguous dot-motion signals.

## 2. Stimulus presentation

The visual stimulator was a 2 GHz Dell workstation running Windows 2000. The stimuli were presented on a 23-inch SONY CRT monitor with $1600 \times 1200$ pixels resolution and 85 Hz frame rate. Luminance values were measured using a Minolta 100 LS Colorimeter by holding the device flush with the monitor, over luminance patches large enough to cover the measuring area. The luminance patches were constructed to match the RGB setting of the stimuli used in each experiment. Observers viewed the stimuli on a black background (0.1 cd/m$^2$) from a distance of 57 cm with their chin in a chin rest. Subjects were required to maintain fixation on a red square (44.7

cd/m$^2$) fixation spot that subtended 0.05° of visual angle. Fixation was ensured using a head-mounted eye-tracker (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 chosen at random from those remaining. The eye-tracker 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.

## 3. Experiment 1

In this first experiment, we examined the perceived speed of rotation for three different sets of ellipses. Each set was defined by the number of dots that were used to define the elliptical contours. By parametrically varying the aspect ratio of the ellipses within each group, we can ask whether or not the speed illusion is observed. Specifically, for each group, we can determine whether 'thinner' dotted ellipses are perceived to rotate faster than 'fatter' ones.

### 3.1. Methods

#### 3.1.1. Observers

Five subjects with normal or corrected-to-normal vision participated in each section of this experiment, thus 15 total subjects were run. One of the authors participated in at least one section of each of the five experiments presented in this paper. For participating in an experiment, naïve subjects were paid $5 for their participation.

#### 3.1.2. Procedure

There were three separate sections to this experiment. Each section tested the perceived speed of rotation of 4 different aspect ratio ellipses (Fig. 1a). In the first section, each ellipse was defined by 12 dots spaced equally along the ellipse's virtual contour. In the second section, the ellipses were defined by 24 equally spaced dots, and in the third section, 32 equally spaced dots were used (Fig. 1b). The dots were positioned so that one dot was placed at the apex of each major and minor axis, and the remaining dots were positioned as to have equal arc-length separation between adjacent dots. This dot placement had the desirable effect of creating a uniform dot-density along the virtual contour of each ellipse.[1]

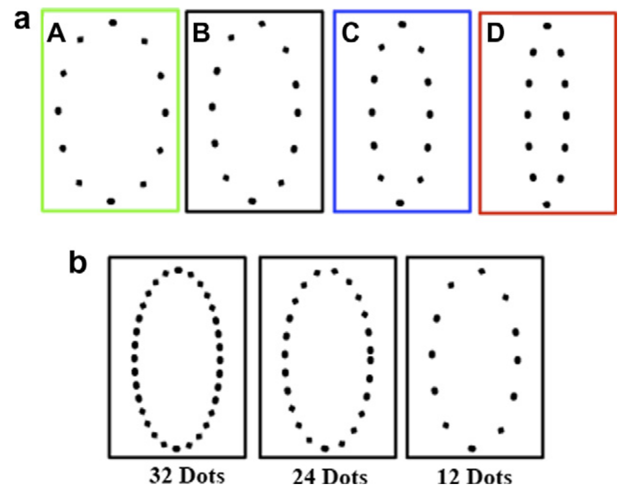


Fig. 1. The basic stimuli. (a) *Experiment 1*. Ellipses were defined by 12 (shown), 24, or 32 small dots spaced equally along a virtual elliptical contour. In each trial a control ellipse (A, Green bounding box) and one test ellipse (either A, B, C or D) were rotated for 500 ms. Each test ellipse had a different aspect ratio. The experiment was designed to test whether or not the thinner ellipses appeared to rotate faster than the rounder ones. (b) *Defining ellipses*. Experiment 1 consisted of three components corresponding to the number of dots (12, 24 or 32) used to define the ellipse. The distance between adjacent dots increased as the number of dots decreased. Note: Unlike the ellipses shown in the figure, the ellipses were defined using white dots on a black background, and were constructed so that the dots were equally spaced around the contour. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Each section of the experiment consisted of multiple trials in which subjects were presented with the stimuli. In each trial, subjects were presented with two rotating ellipses whose contours were defined by very small (0.06°/vis angle (6 pixels wide)) equally spaced white (232.2 cd/m$^2$) dots (12, 24, or 32) presented on a black (0.1 cd/m$^2$) background for 500 ms. Each ellipse was positioned so that its center was located 9 visual degrees along the horizontal axis away from the central fixation spot. Subjects were required to maintain central fixation during the entire 500 ms that the stimuli were presented. One ellipse (control) had the same aspect ratio (=5/3) and same angular velocity (126°/s) on every trial. The other ellipse (test) had an aspect ratio pseudo-randomly selected from the following list which was generated by multiplying the length of the minor axis of the control ellipse by 0.8, 0.6, and 0.4, respectively, yielding aspect ratios of 25/12, 25/9, and 25/6. The test ellipse had an angular velocity pseudo-randomly selected on each trial from the following list: 43°/s, 63°/s, 84°/s, 105°/s, 126°/s, 147°/s, 168°/s, 210°/s. Although both the control ellipse and test ellipse rotated in the same direction, the common direction of rotation was randomly determined for each trial. Subjects were required to indicate, by pressing one of two buttons (2AFC), which of the two ellipses was rotating faster: the one to the left or the one to the right of fixation.

Fig. 1a. illustrates the relative sizes of each of the stimuli used in this experiment. The color of the bounding box around each stimulus (not present during experiments) is used in later figures to distinguish the stimuli. In addition

[1] We use the term 'uniform' dot-density to reflect the fact that the arc-length distance between pairs of adjacent dots is constant around the contour. This leads to the dots being equally spaced along the virtual elliptical contour. However, because the curvature of an ellipse's contour is not constant, this spatial distribution of dots leads to small variations in the Euclidean distance between adjacent dot pairs. These variations are minimal in magnitude compared to the modulations induced by increasing or decreasing the overall number of dots, and thus are unlikely to significantly impact the interpretation of the data presented here.

to trials in which the three test stimuli (Fig. 1a: B, C, D) were used, an additional "control" (Fig. 1a: A) condition was presented in which a test ellipse with the same aspect ratio as the control was us ed. In these trials, the speed of rotation for this "test" ellipse was randomly selected from the list above. This condition, which compares two identical ellipses rotating at various speeds, can be used to test the efficacy and validity of our 2AFC paradigm. Trials were counterbalanced with respect to the side where the control ellipse was presented. Within each run of the experiment (640 trials), 20 trials of each pairing were presented.

The sizes in visual angle of the ellipses used in this experiment were as follows: $4.85° \times 2.91°$, $4.85° \times 2.33°$, $4.85° \times 1.75°$, $4.85° \times 1.16°$ corresponding to the stimuli shown in Fig. 1a: A, B, C, D, respectively. In all cases the ellipses were rotated about their center.

### 3.2. Data analysis

The percentage of times that the test ellipse was perceived to rotate faster than the control ellipse was computed. Thus, for each of the four test ellipses, eight values (one for each angular velocity) were calculated. The corresponding data were then fit with a logit function using a generalized linear model with a binomial distribution in MATLAB. The point of subjective equality (PSE: i.e. the speed at which each test ellipse needs to be rotated in order to be perceived as rotating at the same speed as the control ellipse) was then computed for each aspect ratio for each subject. These values were determined by interpolating the 50% chance level from each of the logit functions fit to the data. A repeated measures ANOVA with a linear contrast was performed in order to determine whether or not perceived rotational speed was parametrically modulated by aspect ratio (the presence of the speed illusion). Mauchly's test for sphericity was performed for each repeated measures ANOVA. Passing a test for sphericity indicates that data are uncorrelated and have homogeneous variance. In every instance, the test was unable to reject the null hypothesis ($p > .2$) that the data sets were spherical, confirming that the variance assumptions made by the repeated measures ANOVA carried out in this study were not violated. For illustration purposes, the mean and standard error of the PSE was computed for each aspect ratio across subjects. These values are used to present the data in the figures for each experiment.

### 3.3. Results

The presence of the speed illusion was tested independently for each of the three ellipse types (12-dot, 24-dot, 32-dot). Data from five different subjects were collected for each group. Fig. 2 illustrates the points of subjective equality for each of the aspect ratios within each of the three groups. The figure demonstrates that the speed illusion was not observed in the 12-dot condition ($F(1,4) = 0.031$, $p < .868$, $\eta_p^2 = 0.008$), and was observed in the 24 ($F(1,4) = 55.692$, $p < .002$, $\eta_p^2 = 0.933$) and 32-dot conditions ($F(1,4) = 28.257$, $p < .006$, $\eta_p^2 = 0.876$).

### 3.4. Discussion of experiment 1

Unlike the motion of a continuous contour, the motion of a single dot is not subject to the aperture problem and is thus entirely unambiguous at the level of the early motion detectors in the visual system. This is true whether the dot lies along a hypothetical, imaginary contour defining a high aspect ratio ellipse or a more rounded one. However, the local motion signal of an individual dot alone is insufficient to determine how fast it is rotating, since the computation of angular velocity must include the distance to the center of rotation. The fact that the speed illusion is not observed in the 12-dot condition demonstrates that this ambiguity alone is insufficient to prevent observers from making accurate estimates of angular velocity across the aspect ratios tested. Despite

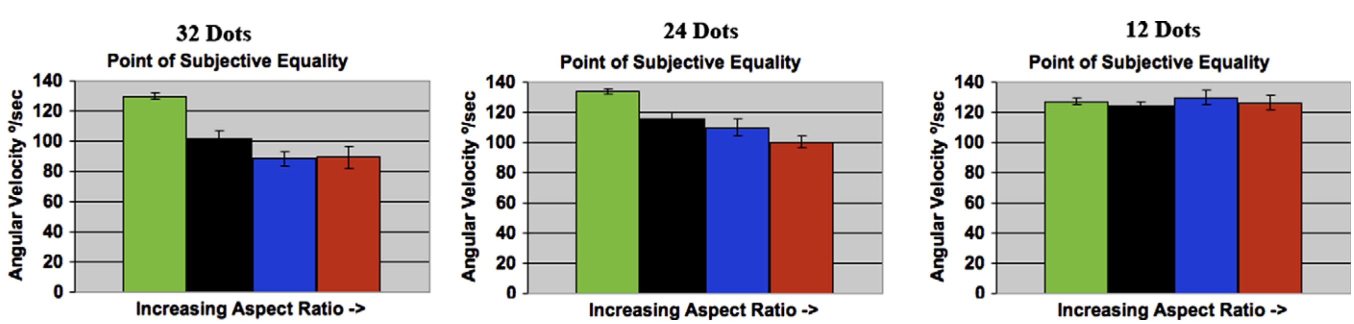


Fig. 2. *Results Experiment 1*. Following the procedure used in our previous study (Caplovitz et al., 2006) of rotational motion, the individual data from each subject were fit with a logit function using MATLAB. For each subject the point of subjective equality at which their corresponding psychometric functions crossed the 50% chance level was interpolated. The ratio of each of the values to the reference speed of the control stimulus (126°) was used to compute how fast each stimulus would need to rotate in order to be perceived as rotating at the same speed as the control ellipse rotating at 126°/s. The presence of the speed illusion would be indicated by the high aspect ratio ellipse (red) needing to rotate much slower than 126°/s in order to be perceived as rotating at this angular velocity. Here we plot the points of subjective equality for each aspect ratio for the 12, 24 and 32-dot ellipses. The error bars represent the standard error of the mean across subjects. The figure illustrates that the speed illusion was observed for the 24 and 32-dot components and not for the 12-dot component. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

the fact that the distance to the origin is not explicit in the local motion signal of an individual dot, each of the four test stimuli was perceived to rotate at the same speed. Based on this observation, we assert that the local-motion of individual dots is unambiguous with respect to the aperture problem and sufficient to construct accurate percepts of rotational motion across aspect ratio.

In contrast to the 12-dot condition, the speed illusion is observed with the 24 and 32-dot configurations. This principal finding indicates that the presence of unambiguous local motion signals alone is not sufficient, in all cases, to drive the overall motion percept. Rather, it appears that in the 24 and 32-dot conditions, the motion percept is driven by emergent motion signals that arise from the virtual contours of the completed ellipses. If the visual system connects the dots into virtual contours, these contours would generate motion signals that not only would not exist in the image, they could be subject to the ambiguity imposed by the aperture problem on moving contours. The following control experiment was designed to rule out potential confounding factor arising from the placement of the dots along the contour with the goal of providing additional evidence that this hypothesis is true.

## 4. Experiment 2

One potential confound arises from the fact that the stimuli used in experiment 1 were designed so that the dots were uniformly distributed around the virtual contours. The actual translational velocities of each dot are directly proportional to their distance from the center of rotation. Because the dots were equally spaced along the virtual contours of each test ellipse, the distribution of actual translational velocities systematically varied across aspect ratio.

In general, the individual dot velocities, and certainly the integral of all dot velocities, will be greater for rounder ellipses than for thinner ellipses. This is because the distance from the center of rotation to a point along the contour will in general be greater for a rounder ellipse than for a thinner one. In this experiment, we examined the perceived speed of rotation for sets of random dot 'clouds' that had the same set of local translational velocities as the ellipses tested in experiment 1.

### 4.1. Methods

#### 4.1.1. Observers

Five subjects with normal or corrected-to-normal vision participated in this experiment.

#### 4.1.2. Procedure

The same overall procedure that was used in experiment 1 was used in this experiment. However, instead of testing all three stimulus groups, only the 24-dot condition was tested. Unlike experiment 1, the dots in this experiment were not placed along virtual elliptical contours. Instead, on every trial, each dot was randomly positioned along the circle of translation that it traversed in experiment 1. This process is illustrated in Fig. 3a. This manipulation preserves the distribution of translational velocities that were present across the aspect ratios tested in the first experiment. However, unlike experiment 1, the dots are no longer grouped into virtual elliptical contours.

### 4.2. Results

The results of this experiment are summarized in Fig. 3b. The figure demonstrates that in fact the opposite of the speed illusion was observed. The random dot clouds corresponding to the fat ellipses were perceived to rotate faster than the random dot clouds corresponding to the thin ellipses ($F(1,4) = 39.61$, $p < .003$, $\eta_p^2 = 0.908$).

### 4.3. Discussion of experiment 2

In experiment 1, the placement of the dots along the virtual contour led to a systematic change in the distribution of local translational velocities across the tested aspect ratios. The results of this control experiment demonstrate that this relationship between aspect ratio and local velocities is not the source of the speed illusion observed in experiment 1. Here, the distribution of local velocities along the virtual contours was identical to those used in experiment 1, and yet the speed illusion was not observed. Interestingly, a different sort speed illusion was observed. Here the random dot clouds corresponding to the fat ellipses were perceived to rotate faster than the ones corresponding to the thin ellipses. This is perhaps not too surprising since the actual distribution of instantaneous dot speeds is greater for the dot clouds corresponding to the rounder ellipses than for those corresponding to the thinner ellipses. These results provide further evidence that the illusory motion percept observed in experiment 1 is constructed by motion signals that arise from the virtual contours of the emergent ellipse. In fact it could be argued that the illusory percepts of experiment 1 were observed *despite* the fact that the low-level motion signals for the rounder ellipses were faster than those for the thinner ellipses.

## 5. Experiment 3

What is the key difference between the 12, 24 and 32-dot conditions tested in experiment 1 that determines whether local dot motion or emergent contour motion will drive the motion percept? Here, there is a potential confound that must be addressed. As the number of dots increases, the spacing between adjacent dots decreases. In experiment 1 the Euclidean distance between adjacent pairs of dots for the 12, 24 and 32-dot conditions was approximately 1.0°, 0.5°, and 0.35° of visual angle, respectively. One hypothesis is that given some maximum number of dots, the percept will be driven by the emergent elliptical contour, regardless of inter-dot distance. An alternative hypothesis is that it is the spacing and proximity of adjacent dots, rather than the

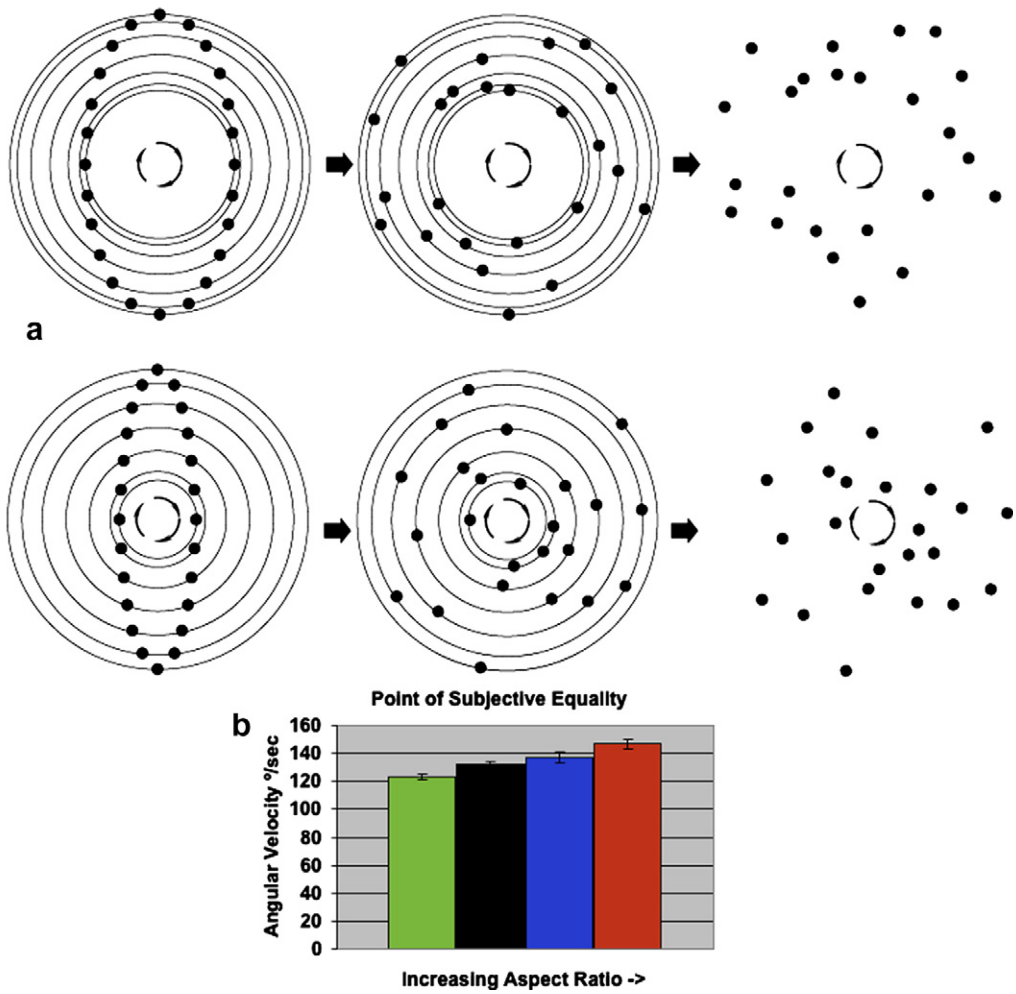


Fig. 3. *Experiment 2*. (a) As each dotted ellipse rotates, the individual dots travel along a circular trajectory in the image. Random dot clouds are constructed by positioning the dots for each ellipse at random locations along the corresponding circular trajectory. As they rotate, the random dot-clouds produce the same set of local translational velocities as those produced when the dots were arranged along elliptical contours. (b) Not only are the dot clouds corresponding to the thinner ellipses not perceived to rotate faster than those corresponding to the fatter ellipses, they are actually perceived to rotate slightly more slowly.

number of dots per se that determines whether dot-motion or emergent contour-motion will drive the percept. In the following experiment, we pit these two hypotheses against one another, in order to be able to rule one of them out. This experiment was designed to test whether it is the number of dots or the distance between dots that is the critical factor in determining whether or not the illusion is perceived. Here we increased the overall sizes of the 24-dot and 32-dot ellipses used in experiment 2, thereby increasing the distance between adjacent dots while keeping the number of dots fixed.

### 5.1. Methods

#### 5.1.1. Observers

Five subjects with normal or corrected-to-normal vision participated in each component (24 or 32-dot ellipses) of this experiment, thus 10 total subjects were run.

#### 5.1.2. Procedure

The same overall procedure that was used in experiment 2 was used in this experiment. However, instead of testing all three stimulus groups, only the 24 and 32-dot conditions were tested. Here, the overall sizes of the ellipses used in experiment 2 were increased by a factor of 1.5. This had the effect of increasing the linear distance between adjacent dots by a factor of 1.5, while preserving the aspect ratios of each ellipse. In the case of the 24-dot ellipse, the inter-dot distance was somewhat smaller ($\sim$0.75°) than the inter-dot distance that existed in the 12-dot ellipses used in prior experiments. In addition, the inter-dot distance in the large 32-dot condition was slightly greater ($\sim$0.53°) than that in the original 24-dot condition. Thus the inter-dot intervals used in these new larger stimuli were intermediate to those examined in the original 12 and 24-dot conditions. The size of each ellipse-defining dot was the same as in experiment 2 (0.06 visual degrees).

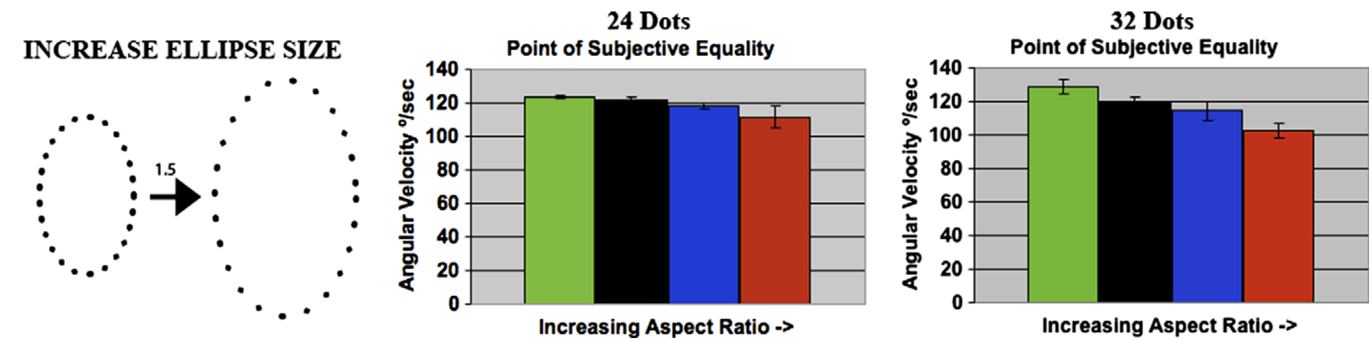


Fig. 4. *Experiment 3*. Here the size of the ellipses used in the 24 and 32-dot sections of experiment 2 was increased by a factor of 1.5, thereby increasing the distance between adjacent dots. This had the effect of making all four aspect ratios in the 24-dot condition appear to rotate at the same subjective speed (compare middle column to Fig. 2b middle column). In contrast, the speed illusion is still observed in the 32-dot condition (right column). This suggests that dot spacing and not the number of dots is critical in determining whether or not the dot motion will drive the percept.

### 5.2. Results

Fig. 4 illustrates the PSEs for each of the aspect ratios within the 24 and 32-dot stimulus groups. Here we see that the speed illusion that was present in experiments 1 and 2 is no longer present in the case of 24 dots ($F(1,4) = 4.051$. $p > .114$, $\eta_p^2 = 0.503$). That is to say, in the 24-dot group, when the distance between dots was increased, each of the four aspect ratio ellipses was perceived to rotate at the same angular speed. This result makes clear that spatial proximity is the critical factor in determining whether or not the local motion of the dots will drive the rotational motion percept. In contrast, the speed illusion is still observed in the 32-dot stimulus group ($F(1,4) = 13.281$, $p < .022$, $\eta_p^2 = 0.769$), this is presumably true because, although the dot spacing has been increased in this condition, the dots are still sufficiently close together to drive the illusory percept. It is interesting to note that the pattern of PSEs across aspect ratio in this condition more closely resembles that observed in the 24-dot condition from experiment 2 rather than the 32-dot condition which reflects the increased dots spacing in the large 32-dot condition.

The results of this experiment conservatively place the critical inter-dot distance for determining whether local-dot or emergent virtual contour motion information will drive the motion percept in this paradigm between 0.5° and 0.8° of visual angle. This result is also useful in ruling out the possibility that the size increase by itself can explain the loss of the illusory percept in the 24-dot condition.

## 6. Experiment 4

The results of experiments 1 and 3 suggest that the critical factor in determining whether or not the speed illusion will be perceived is the distance between adjacent dots. One hypothesis for why this might be is that for neurons tuned to low spatial frequencies, the dotted contour is indistinguishable from a continuous contour. Fig. 5 illustrates how a dotted contour would appear if observed only through low spatial frequency channels. It is possible that if the dots are close enough, as in the 24 and 32-dot conditions, the low spatial frequency channels produce motion signals consistent with continuous contours whereas, if the dots are far enough apart, they do not. Such low spatial frequency blurring has been hypothesized to underlie several form-based illusions (Ginsburg, 1971, 1975, 1979, 1984; Ginsburg & Evans, 1979) such as the Mueller-Lyer illusion (Carrasco, Figueroa, & Willen, 1986). In order to address whether the low spatial frequency channels are responsible for the presence of the speed illusion when the dots are closely spaced, we used ellipses defined by 32 contrast-balanced dots, to which the low spatial frequency channels are essentially blind (Carlson, Anderson, & Moeller, 1980).

It should be noted that the contrast balancing of dots serves to "high-pass" filter the frequency content of corresponding non-balanced dots. The cutoff frequency for this filter will be a function of the overall size of the dot itself. The larger the dot, the lower spatial frequency content there will be. However, the assumption underlying the contrast-balanced dot is that any luminance-sensitive neuron whose receptive field is at least as large as the entire dot, will not detect any net change in the mean spatial luminance, thus making the dot 'invisible' to that neuron. This suggests that the contrast-balanced dot should be invisible to any neuron whose receptive field is at least as large as the dot itself, which satisfies our requirement that individual dots not be 'blurred' into a continuous contour by low spatial frequency neurons with large receptive fields. In the extreme case, one can consider a scenario in which a low spatial frequency neuron (e.g. one with a large receptive field) only partially overlaps with the contrast-balanced dot. In this extreme case the mean spatial luminance across the receptive field will indeed be predicted to deviate slightly from the background. As such, it is possible that some activity within low spatial frequency channels could persist, albeit at an extremely attenuated level relative to non-contrast balanced dots.

### 6.1. Methods

#### 6.1.1. Contrast balanced dots

Each dot consisted of a white (232.2 cd/m$^2$) center (radius 0.06° visual angle) surrounded by a black (0.1 cd/m$^2$) annu-

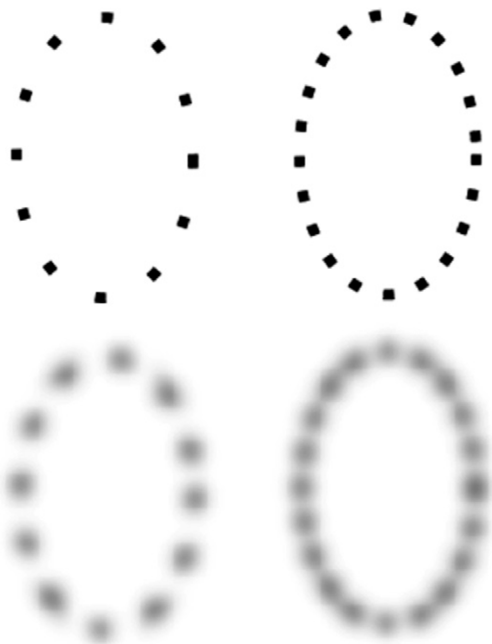

Fig. 5. Low spatial frequency "blurring" It has been hypothesized that several form-based illusions can be predicted by how the low spatial frequency channels "view" the stimulus. In our previous work (Caplovitz & Tse, 2006a, 2006b) we demonstrated that the speed illusion is present for continuous contours. One hypothesis concerning why the speed illusion is observed in the 24 and 32-dot conditions tested in this study is that when the dots are close together, the low spatial frequency channels "see" a continuous contour (right-hand column). According to this hypothesis, when the dots are farther apart (left-hand column), the contour is still discontinuous even when "viewed through" the low spatial frequency channels.

lus (radius 0.10° visual angle). The dots were placed on a grey background (96.9 cd/m$^2$). The luminance of the grey background was chosen so that the mean spatial luminance of each contrast balanced dot was matched to the luminance of the background (see Fig. 6). The circular nature of each dot was only approximate due to the pixilated nature of the CRT monitor used to display the stimuli. As mentioned above, while it may be theoretically impossible to make the stimuli completely invisible to all low spatial frequency neurons, it should be noted that under these conditions the screen appeared a uniform grey when viewed from a distance greater than 57 cm, suggesting that any residual activity within low spatial frequency channels was in fact minimal.

### 6.1.2. Observers

Five subjects with normal or corrected-to-normal vision participated in this experiment.

### 6.1.3. Procedure

The same overall procedure that was used in experiment 1 was used in this experiment; however, only the 32-dot (closely spaced) condition was tested, and the ellipses were defined using contrast-balanced dots.

### 6.2. Results

Fig. 6 illustrates the points of subjective equality for each of the aspect ratios within the stimulus group. Here we see that the speed illusion that was present in experiments 1 and 2 is still present ($F(1,4) = 93.484$, $p < .001$, $\eta_p^2 = 0.959$). That is to say, even when the stimuli were constructed to be invisible to the low spatial frequency channels that would likely be involved in 'blurring' neighboring dots into a continuous contour, the thinner ellipses were perceived to rotate faster than the fatter ellipses.

## 7. Experiment 5

The results of the previous experiments suggest that when the contour-defining dots are close enough together, the speed at which the ellipses are perceived to rotate is driven by the emergent properties of the contour that the dots create, rather than by the dots themselves. In this final experiment, we directly compare the perceived motion of ellipses defined by dotted contours with those defined by continuous contours. This experiment consisted of two sec-

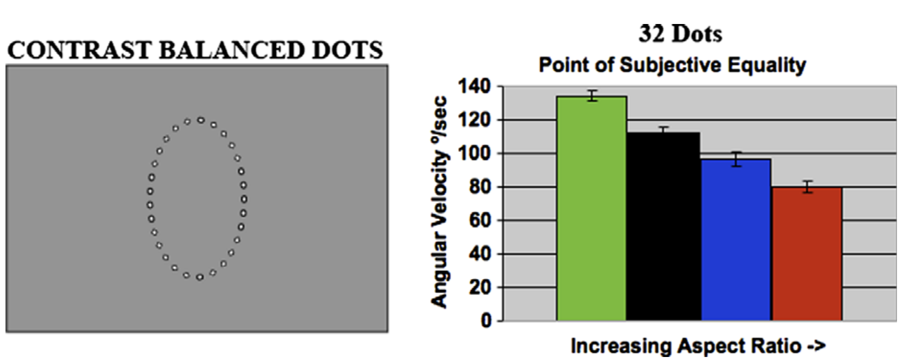


Fig. 6. *Experiment 4*. In order to rule out low spatial frequency "blurring" (see Fig. 5), contrast balanced dots were constructed by superimposing small white dots on top of larger black dots. These "annuli" were then presented on a grey background, whose luminance was chosen to match the mean spatial luminance of the dots. This has the effect of making the dots 'invisible' to low-level neurons tuned to low spatial frequencies. These contrast-balanced dots were tested in the 32-dot condition. The speed illusion was again observed, demonstrating that low spatial frequency "blurring" is not the reason why dot proximity predicts the motion percept.

tions. In the first section we compared continuous contour ellipses with ellipses defined by 12 dots, and in the second section we compared the continuous contour ellipses with ellipses defined by 32-dots. These two sections allow us to examine the relationship between continuous contour ellipses and dotted ellipses that either do or do not exhibit the speed illusion.

### 7.1. Methods

#### 7.1.1. Observers

Five subjects with normal or corrected-to-normal vision participated in each section of this experiment, thus 10 total subjects were run.

#### 7.1.2. Procedure

A similar paradigm to that used throughout the previous experiments was used in this experiment with two main differences. The first of these differences was that the control ellipses presented in each of the trials were always defined by a continuous contour whose thickness (0.12° visual angle) matched the diameter of the contour-defining dots (same as those used in experiments 2 and 3) of the test ellipses. The second of these differences was that the control and test ellipses (either 12 dots in section one, or 32 dots in section two) always had the same aspect ratio (chosen at random from the set of four tested in all previous experiments) on every trial. Thus, this experiment directly compared the perceived speed of two ellipses (one continuous and one dotted) with the same aspect ratio, and made this comparison for each of the four aspect ratios tested throughout this paper for both the 12 and 32-dot conditions.

### 7.2. Results

The results of this experiment are shown in Fig. 7a and b, which illustrate the points of subjective equality for each aspect ratio for ellipses defined by 12 and 32-dots, respectively. As is made clear in Fig. 7a, when the test ellipses were defined by 12 dots, there is a systematic relationship between aspect ratio and PSE ($F(1,4) = 92.16$, $p < .001$, $\eta_p^2 = 0.958$). Specifically, the lower the aspect ratio of the dotted ellipse, the faster it is perceived to rotate relative to the continuous contour. While somewhat unintuitive, this is precisely what one would expect considering that there is no speed illusion observed in ellipses defined by 12 dots (the illusion is observed using continuous contours). When 12 dots are used to define the contour, all four aspect ratios are perceived to rotate at the same speed; however as the aspect ratio of the continuous contour control ellipse decreases, so does its perceived speed of rotation. Thus as the aspect ratios decrease, the continuous contour ellipses appear to slow down relative to the dotted contoured ones.

In contrast, when 32 dots are used to define the test ellipses (Fig. 7b), little or no systematic relationship between aspect ratio and PSE is observed ($F(1,4) = 4.319$, $p > .106$, $\eta_p^2 = 0.519$). This indicates that for each aspect ratio, both the dotted and continuous ellipses are perceived to rotate at nearly the same angular velocity, which is exactly what one would expect considering that both sets of ellipses produce the speed illusion. This supports the hypothesis that the underlying source of the speed illusion observed with rotating dotted ellipses is the same as that for rotating ellipses that possess continuous contours, despite the divergent nature of their low-level motion signals.

## 8. Discussion

### 8.1. Summary of results

The purpose of this research was to investigate factors that influence the perception of objects undergoing rotational motion. In past work (Caplovitz et al., 2006) we have shown that the perceived angular velocity of rotating ellipses is a function of aspect ratio. In particular, thin ellipses

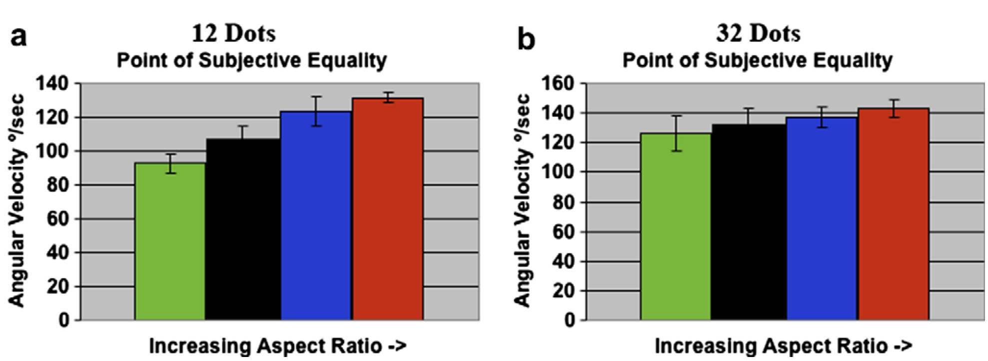


Fig. 7. *Experiment 5*. Continuous and dotted contour ellipses were directly compared in this experiment. In (a) we see that as the aspect ratio of ellipses defined by 12 dots decreases, their perceived speed systematically increases relative to continuous contour ellipses with the same aspect ratio. This occurs because the speed illusion that is observed with continuous contours is not observed with the 12-dot contours. In contrast, no systematic relationship is observed in the 32-dot condition shown in (b). This is because the speed illusion is observed in both the continuous and 32-dot contours, indicating that the perceived speed of the dotted ellipses relative to the continuous ellipses does not modulate as a function of aspect ratio.

tend to be perceived to rotate faster than fatter ellipses rotating at the same objective angular velocity. Here we constructed ellipses out of dots whose motion signals should be immune to the ambiguities imposed by the aperture problem. By investigating the circumstances under which the motion of the global figure is misperceived, we can gain insight into the roles of local and global motion signals in generating motion percepts. Because the motion of an individual dot is unambiguous, the presence of such a speed illusion suggests that the motion percept is not being driven by the local motion signals of the dots per se, but rather by the emergent properties of the elliptical contour that is constructed from the moving dots by grouping procedures. That is, our motion perception appears to be influenced by motion signals that arise from inferred form information, such as the virtual contours of grouped dots. Thus motion perception is influenced by motion signals of constructed entities that do not explicitly exist in the image. The data presented here lead to two principal findings. The first is that the presence of the speed illusion is dependent upon the visual angle subtended between adjacent dots. The second finding is that the speed illusion is not specifically generated from motion signals arising from low spatial frequency channels, and thus does not result from a 'blurring' of the dots into a continuous contour.

We interpret the absence of the speed illusion in the 12-dot case to indicate that the global percept of the rotating ellipse is generated solely by the unambiguous motion signals generated by the dots. Conversely, when the illusion is present, we conclude that the percept of rotational speed is generated by the emergent virtual contours of the ellipse itself and is not driven solely by the local motion signals of the dots.

These findings are consistent with recent research (Bex, Simmers, & Dakin, 2003; Verghese, McKee, & Grzywacz, 2000) that has investigated the interaction between dot motion and the perceived motion of emergent contours. These studies found that particular configurations of coherently moving dots could influence the threshold at which the emergent figure they defined could be detected within noise. Of particular note, dot spacing and number of dots defining the contours were found to be key factors in determining thresholds independent of frequency content. The findings presented here extend upon previous work by illustrating that the grouping processes that appear to govern the ability to detect emergent contours can lead to the generation of motion signals that are themselves seemingly independent of the low-level motion signals that drive the grouping process itself. It is as if detected motion signals are used to generate higher-order (global form-based) motion signals that in turn underlie perceived motion, whereas the lower-order detected motion signals are not directly used to generate motion perception. Only when the higher-order motion signals fail to be generated, because dot spacing is too large, is motion perception based upon the lower-order motion signals. If virtual contours can be generated, their ambiguous motion signals apparently trump the unambiguous motion signals that arise from individual dots. It is as if the visual system discards local motion information in favor of more global, emergent motion signals, even though the motion signals of emergent virtual contours are more ambiguous than the original dot motion signals.

### *8.2. The integration of local signals and the possible role of component vectors*

It has been hypothesized that global motion percepts arise through the integration of low-level motion signals. For objects defined by smooth, continuous contours, many low-level motion signals are ambiguous due to the aperture problem. It has been asserted that the ambiguity of the aperture problem can be overcome by the integration of local motion signals (Adelson & Movshon, 1982; Bowns, 2001, 2002; Hildreth, 1984; Lu & Sperling, 1995, 2001; Yo & Wilson, 1992 ). For the case of a continuous contour, the motion signal at a given location will always be perpendicular to the contour at that point. These "component signals" serve as the basic detected features from which the integration system must construct the true velocity signals. As we described in our previous work (Caplovitz et al., 2006), the perception of rotational motion is particularly difficult to account for on the basis of local motion signals. In particular, such an integration system would have to account both for the perception of rigid rotation and for the speed illusion.

Despite the fact that no local integration model yet exists that can predict how an object will appear to move under all circumstances, this does not imply that a local-motion integration system does not exist. Indeed, one could assume that such a system does in fact exist, and that in the case of the dotted contours, when the dots are close enough together, the unambiguous signals they produce, get integrated as if they were generated at locations along a continuous contour, thereby producing the speed illusion. We believe that this possibility is unlikely to be the case for the following reasons.

Unlike the case for a continuous contour, the low-level motion signals generated by individual dots (forming an elliptical contour) will not be perpendicular to the virtual contour on which they are positioned. Rather these motion signals will lie in the direction tangent to the circle transcribed by the dots as the elliptical contour rotates. As such, the set of motion signals that would be available to any potential integration system are fundamentally different in the two cases (dotted and continuous contours) and would thus predict two very different percepts. This discrepancy is illustrated in Fig. 8 which shows the unambiguous tangential motion signals generated by two points along a dotted contour, and the ambiguous component motion signals generated at, and in a direction perpendicular to, the corresponding locations along a continuous contour. As can be seen in the figure, these pairs of motion signal are quite different from each other. Thus one would

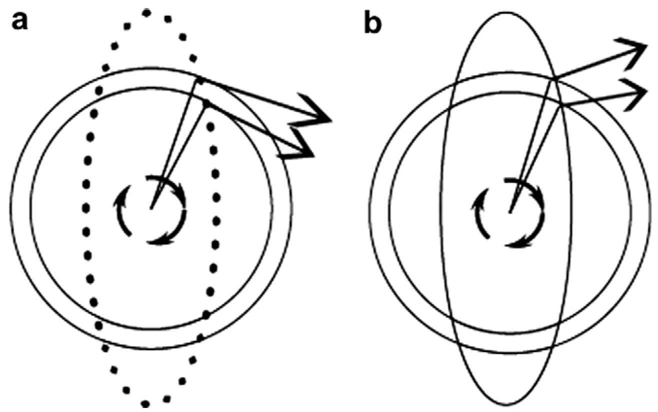


Fig. 8. *Low-level motion signals*. A dotted ellipse (a) will be perceived to rotate in the same manner as a continuous ellipse (b) if the defining dots are close enough together. However, the low-level motion signals produced by the two ellipses are quite different, both in direction and in magnitude. The unambiguous motion of the dots result in velocity vectors tangent to the circle transcribed by the dots as the ellipse rotates. In contrast, for a continuous contour shown in (b), the only detectable motion signals are the projections of the tangential velocity vectors in (a) onto the vector normal to the elliptical contour at that point (component vector). Unless the contour is a straight line, these vectors must necessarily be smaller and point in a different direction than those in (a).

predict that the outputs of any integration system would be different provided these differing inputs. However, phenomenologically speaking, the percepts of rotating ellipses defined by dotted or continuous contours are the same, both in the rigid nature of the rotation, and the relative speed at which the ellipses are perceived to rotate, as shown by the presence of the speed illusion (provided the dots are spaced closely enough together; see experiment 5). Based on this observation, we conclude that the integration of low-level motion signals is not solely responsible for the percept of a rigidly rotating ellipse, either with a continuous or dotted contour, and is not solely responsible for the speed illusion that accompanies it.

### 8.3. Trackable features

Rather than relying on the integration of local motion signals, we hypothesize that in the case of both dotted and continuous ellipses, the percept of a rigidly rotation is generated by the tracking of specific, unambiguous motion sources. Ullman (1979) first suggested that the aperture problem could be overcome in this fashion.

Recent neurophysiological data have shown that neurons in macaque MT respond more to terminator motion in a barber pole stimulus than to the ambiguous signals generated by portions of the contour away from terminators; Furthermore, they respond more to intrinsically owned terminators than to extrinsic terminators (Pack, Gartland, & Born, 2004). It has also been shown that neurons in macaque MT will initially respond to the direction of motion that is perpendicular (component direction) to a moving line independent of the actual direction of motion (Pack & Born, 2001). These same neurons will, over a period of ~60 ms, shift their response properties so that they respond to the true motion of the line independent of its orientation, suggesting that the unambiguously moving endpoints of the line are quickly but not instantaneously exploited to generate a veridical motion solution. The response properties of these neurons match behavioral data that show that initial pursuit eye-movements will be in the direction perpendicular to the moving line, and then rapidly adapt to follow the direction of veridical motion as defined by the line terminators (Pack & Born, 2001). There is also neurophysiological evidence of end-stopped neurons in V1 that respond to the motion of line-terminators independently of the line's orientation (Pack, Livingstone, Duffy, & Born, 2003), suggesting that form-based trackable features such as line terminators can be directly extracted from the image as early as V1. Such cells are largely immune to the aperture problem.

Furthermore, there is neurophysiological evidence from macaques that the coherent motion of dots creating an emergent contour can directly stimulate neurons in early visual cortex. These same neurons responded much less or not at all to dot arrangements that were presented in which human observers did not perceive distinct emergent contours (Peterhans, Heider, & Baumann, 2005). This suggests that the neurophysiological basis for the tracking of form-based features derived from continuous contours could in theory apply to those contours that emerge from the coherent motion of individual dots. This is also consistent with neurophysiological data from single cells in monkey that shows that neurons as early as V1 and V2 (but mostly in V2) respond to illusory contours (Grosof, Shapley, & Hawken, 1993; Peterhans & von der Heydt, 1991; von der Heydt, Peterhans, & Baumgartner, 1984; von der Heydt & Peterhans, 1989). More recently, non-invasive neuroimaging techniques such as PET and fMRI have found representations of illusory contours within V2 in humans (ffytche & Zeki, 1996; Hirsch et al., 1995; Larsson et al., 1999). It should be remembered that motion-tuned neurons do not respond to the image, but rather respond to their inputs. Once an illusory contour has been constructed, motion sensitive neurons that receive that illusory contour signal as input should respond to the motion of that illusory contour as they would to the motion of a real contour.

In the case of the 12-dot ellipse or large 24-dot ellipse, in which no speed illusion is observed, the trackable features seem to be the dots themselves. Because the motion of the dots is unambiguous and independent of the aspect ratio they define, no speed illusion is observed. However, when the dots are close enough together, the hypothesized feature tracking system is presumably unable to lock onto the motion of a single dot. Rather, we hypothesize that the system instead locks onto features of the emergent elliptical figure, namely the regions of high contour curvature located at the ends of the major axis of the ellipse. As such, the dotted ellipses get processed in the same way as ellipses defined by continuous contours, and the speed illusion is observed. The percept is driven by motion signals generated by changes in position of the emergent contour, rather than by the unambiguously moving dots from which those contours must be constructed.

Based on the findings of this study, we conclude that if the unambiguous local motion of the contour-defining dots cannot be spatially isolated, the resultant global motion percept is driven by the grouped form of the object undergoing rotation. In this case, the motion of the dots is deemphasized or even discarded in favor of motion signals arising from the emergent elliptical contour. On the other hand, global percepts of rotating objects can be driven by the unambiguous local motion of the dots, provided that such motion signals can be spatially isolated and are not 'masked' by grouping procedures.

These results make evident that a clear distinction should be made between stages of detection and stages of construction in visual processing. Early neuronal processing is no doubt primarily involved in detecting different types of stimulus (e.g. motion, luminance, or orientation) 'energy,' while later neuronal processing is involved in 'connecting the dots' that have been detected into meaningful and hopefully veridical representations of events in the world. Again, neurons respond to their immediate inputs rather than responding directly to the contents of the image. If a stage of grouping creates the (actually untrue) information that a contour exists and is moving, cells downstream that receive information that a contour is moving will respond as if a contour were really there in the image. These cells could potentially suffer from the same sorts of limitations that may hinder the processing of continuous contours (such as the aperture problem or the ability to identify and track contour features). The evidence provided here suggests that this could be true even though earlier cells that detect the dots do not suffer from the ambiguities created by the aperture problem. Although it is commonly assumed that the aperture problem is a problem faced by motion units in the earliest stages of detection, the present results indicate that there are circumstances that are quite the opposite, where the aperture problem or other potential sources of motion ambiguity may only emerge as a consequence of constructive procedures that must occur subsequent to stages of detection.

In a recent neuroimaging study (Caplovitz & Tse, 2006a) we found evidence that BOLD signals in visual area V3A as well as the Lateral Occipital Complex (LOC) were modulated by the degree of contour curvature present in rotating stimuli. These modulations were independent of both the magnitudes of the low-level motion signals and the perceived speed of rotation. This finding suggests that form processing in V3A and the LOC is involved in the 'construction' of higher-level motion signals rather than in the 'detection' of stimulus driven low-level motion signals.

This is not to say that the illusion of perceived rotational speed is solely the result of the aperture problem or local component motion signals. In past work (Caplovitz et al., 2006) we showed that the magnitude of perceived rotational speed can be well accounted for by integrating local component motion signals along the contour of the ellipse. However, a purely component solution should yield the percept of a gelatinously moving ellipse rather than one of a rigidly rotating ellipse. Since a rigidly rotating ellipse is perceived, more must be going on than such an integration of component motion signals, whether along a real contour or along a virtual contour defined by grouped dots. In particular, the motion signals arising from trackable features such as corners or regions of high curvature may dominate component motion signals when they exist in the image.

An irony of the present results is that the visual system appears to ignore or discard the unambiguous motion signals arising from the individual dots. Instead, the visual system seems to rely on the motion signals of the virtual contours it constructs from the dots, leading to false estimates of angular velocity. Our conscious experience of motion appears to be driven primarily by this higher-order derived set of motion signals, at least for the class of stimuli considered here.

## Acknowledgments

We thank Omar Pardesi and R. Randall McKnight for their assistance in collecting the data for this project. This project was funded by NIH Grant R03 MH0609660-01 grant to P.U.T. and by a predoctoral NSF fellowship 2005031192 to G.P.C.

## Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.visres.2006.12.022.

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