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Illusory contour strength does not depend on the dynamics or relative phase of the inducers

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Abstract

We use a new objective measure of illusory contour strength, threshold reduction for aspect ratio discrimination, to examine the effect of dynamics and relative phase on the Kanizsa illusion. We found no dependence of illusory contour strength on the relative phase of flickering inducers (in phase, antiphase, or in quadrature phase) either for the standard Kanizsa square, or for modifications that facilitated or interfered with amodal completion. Comparison with a vernier acuity task indicates that the distance between the inducers, rather than the nature of the task, accounts for the insensitivity to relative phase. © 2000 Published by Elsevier Science Ltd.

Keywords: Illusory contours; Hyperacuity; Temporal phase

1. Introduction

Illusory contour formation (Kanizsa, 1976; Prazdny, 1985) and hyperacuity judgments (Westheimer, 1981; Klein & Levi, 1985) highlight the great spatial specificity with which visual inputs can be combined. Vernier alignment thresholds are elevated for static targets whose components have opposite polarity (Mather & Morgan, 1986; Levi & Westheimer, 1987; O'Shea & Mitchell, 1990) compared with targets whose components have like polarity. Such stimuli may be considered the low-frequency limit of antiphase and in phase flickering stimuli. For vernier targets with flickering components, relative phase indeed has a dramatic effect on alignment thresholds (Victor & Conte, 1999), most prominently below 4 Hz.

However, it is unclear whether relative phase has an analogous effect on illusory contour formation. Initial studies based on a subjective measure of illusory contour strength (Shapley & Gordon, 1983, 1985; Grossberg & Mingolla, 1985) found no effect of the relative polarity of the inducers, while later studies, based on a formal rating scale or saliency in a search task, found a diminution in strength with opposite-polarity inducers (Matthews & Welch, 1997; Spehar, 1998; He & Ooi, 1998a,b). For stimuli with dynamic inducers, a study based on comparison of synchronous and asynchronous alternatives found no effect of component dynamics (Fahle & Koch, 1995), while one based on adjustment and rating (Kojo, Liinasuo, & Rovamo, 1993) found a modest effect.

In this study, we re-examine the effect of stimulus dynamics on illusory contour strength. We concentrate on the frequency range and relative phases in which the effect of dynamics on vernier alignment (Victor & Conte, 1999) is most marked (1–4 Hz). We use a readily quantified measure of illusory contour strength, that is objective and demonstrably graded, albeit indirect. With this approach, we find no effect of component asynchrony on illusory contour strength for flickering stimuli. We also show that a simple modification of the vernier stimulus, namely, introduction of a gap between components, eliminates the effect of relative phase on alignment thresholds. This demonstrates that the differences in dynamics of vernier alignment and illusory contour formation depend on the spatial separation of the stimulus components, rather than on the nature of the task (e.g. binding vs. alignment, or all-or-none vs. graded).

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2. Methods

2.1. Subjects

Studies were conducted in three male and six female normal subjects, ranging in age from 20 to 45. Three experienced psychophysical subjects (MC, EM, YLF) participated in all experiments and at least one naive observer participated in Experiments 1–3. All subjects had visual acuities (corrected if necessary) of 20/20 or better.

2.2. Display

These visual stimuli were produced on a Sony Multiscan 17seII monitor, with signals driven by a PC-controlled Cambridge Research VSG2/3 graphics processor. The resulting 768 × 1024 pixel display had a mean luminance of 47.2 cd/m^2, a refresh rate of 100 Hz, and subtended 6.4 × 8.6 deg (0.5 min per pixel) at the viewing distance of 200 cm. The intensity versus voltage behavior of the monitor was linearized by photometry and lookup table adjustments provided by VSG software.

2.3. Illusory contour stimuli

The basic Kanizsa (1976, 1979) square stimulus had a contrast of 0.50, an edge length $L = 3$ deg, and an inducer radius $R = 0.75$ deg, yielding a support ratio ([real contour length]/[edge length] $= 2R/L$) of 0.5. Displays consisted of the inducer tokens of a Kanizsa square, slightly displaced to create an illusory rectangle. Subjects judged whether this rectangle was in a 'portrait' or 'landscape' orientation. We determined the threshold aspect ratio for this shape judgment in the standard Kanizsa configuration (in which the inducers were rotated inward, permitting the formation of an illusory contour), and for a configuration in which the inducers were rotated outward (preventing the formation of the illusory contour). In both cases, the inducers were presented with luminance polarities that were in phase or antiphase. These four combinations are shown in Fig. 1A. As explained below, our index S for the strength of the illusory contour is the reduction in the threshold log aspect ratio for shape discrimination when a potential illusory contour is present ($\ln r_{in}$), compared with when it is absent ($\ln r_{out}$), i.e. $S = (\ln r_{out})/(\ln r_{in})$. $S = 1$ corresponds to no measurable

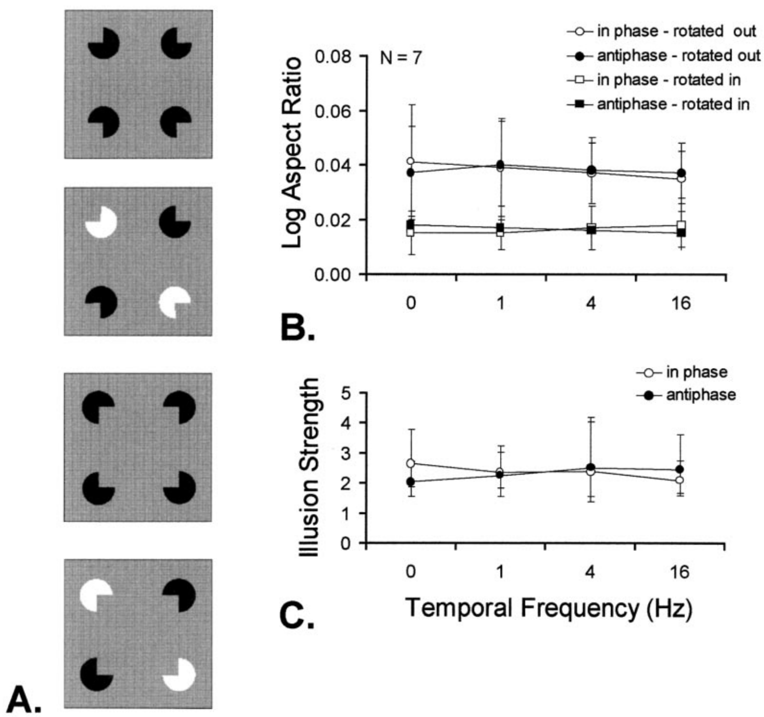

Fig. 1. (A) Illusory contour stimuli. From top to bottom, inducers presented in phase rotated out, antiphase rotated out, in phase rotated in, antiphase rotated in. (B) Mean threshold log aspect ratios $\ln r_{out}$ (circles) and $\ln r_{in}$ (squares) for shape discrimination with inducers presented in phase (open symbols), and in antiphase (filled symbols). Error bars represent ± 2 S.E.M., calculated across subjects' individual means of $\ln r_{in}$ and $\ln r_{out}$. (C) Illusion strength $S = (\ln r_{out})/(\ln r_{in})$ derived from data of panel B. Open circles, inducers in phase; filled circles, inducers in antiphase. Error bars represent ± 2 S.E.M., calculated across subjects' individual measures of S. Support ratio 0.5, contrast 0.5. $N = 7$.

effect of the putative illusory contour; values of $S > 1$ correspond to progressively stronger effect of the contour.

2.4. Vernier stimuli

Stimuli consisted of two horizontal bars (0.5–2 deg long), with or without a horizontal gap. Bars had a Gaussian profile (full width at half maximum 0.125 deg). Subpixel vertical displacements d were produced by shifting the Gaussian bar profiles pixel by pixel (Krauskopf & Farell, 1991; Victor & Conte, 1999).

2.5. Psychophysical methods

Stimuli were presented for 1 s, under an envelope that ramped on and off over 30 ms at onset and offset (Victor & Conte, 1999). Staircases consisted of two preliminary reversals in which the parameter of interest (log aspect ratio $\ln r$ or displacement d) was changed by 0.3 log units, followed by ten reversals with a step size of 0.1 log units. The threshold estimate from each staircase was the geometric mean of eight reversals (the final ten reversals with one high and one low outlier excluded). The parameter value was decreased following two successive correct judgments, and increased by the same factor following each incorrect judgment, providing an estimate of the parameter required for 71%-correct judgments. Five (Experiment 1) or six (Experiments 2–4) staircases were combined (geometric mean) to obtain each subject's threshold for each condition. Within each experiment, staircases for the several conditions were interleaved and counterbalanced within and across subjects. Brief practice sessions sufficed to attain stable performance. Trials were self-paced, and organized into sessions of 20–36 staircases, lasting 1–2 h. The typical staircase contained 50–60 judgments.

For illusory contour experiments, each trial consisted of two successively-presented stimulus intervals (500 ms interstimulus interval) with aspect ratios differing by a factor of r, one in 'portrait' orientation (V:H $= r^{1/2}$), and the other in 'landscape' orientation (V:H $= r^{-1/2}$). The subject was asked to identify which interval contained the figure that was closer to a 'landscape' orientation. This two-interval approach was used to avoid erroneous judgments due to subtle geometrical distortions of the display or observer bias. The position of the stimuli relative to the center of the display was jittered from trial-to-trial (15% of side length L) to prevent the use of the edge of the frame as a cue to position or shape. To avoid the use of unintended spatial cues such as the absolute or relative sizes of the gaps, the nominal side length L of the illusory square was jittered from trial-to-trial (15% of side length L) and the radii of the inducers R were independently jittered from trial-to-trial (10% of side length L).

For vernier experiments, each trial consisted of a single stimulus interval containing a standard vernier bar pair, with one of the horizontal bars displaced by an amount d. The subject was asked to indicate which bar was displaced upward. Bar positions were jittered as above to eliminate the use of the borders of the display as an absolute positional cue.

Unless otherwise noted, statistical comparisons between conditions were based on one-tailed paired t-tests across subjects, without correction for multiple comparisons.

3. Results

3.1. Experiment 1: dependence of illusory contour strength on inducer dynamics

Fig. 1B shows aspect ratio thresholds for static inducers and flickering inducers presented at 1, 4, and 16 Hz. For inwardly-rotated inducers, the mean threshold log aspect ratio $\ln r_{in}$ was 0.01–0.02 (Fig. 1B, filled circles). For outwardly rotated inducers, the mean threshold log aspect ratio $\ln r_{out}$ was 0.03–0.04 (Fig. 1B, open circles). This increase in aspect ratio threshold, consistent with the observations of Regan and Hamstra (1992), indicated that shape discrimination improved when an illusory contour was present, compared with performance on a similar task in which illusory contours were absent. When the phase of one pair of diagonally-opposing inducers was reversed, the log aspect ratio thresholds at 1, 4, and 16 Hz were unchanged ($P > 0.19$ for $\ln r_{in}$ and $\ln r_{out}$ at the three flicker frequencies) across the individual subjects ($N = 7$). However, for static stimuli, this phase reversal caused a slight but statistically significant ($P = 0.035$) increase in log aspect ratio $\ln r_{in}$ compared with the in phase condition.

The ratio $S = \ln r_{out}/\ln r_{in}$ expresses the improvement in aspect ratio threshold when illusory contours are present, and is therefore taken to be a measure of their strength. This ratio was 2.5–3 (Fig. 1C) for flickering inducers at the three temporal frequencies studied, for both in phase (open circles) and antiphase (filled circles) conditions. However, for static inducers, there is a small (30%) but significant decrease in illusion strength for the antiphase condition compared with the in phase condition ($P = 0.022$).

We also examined the effect of 'quadrature phase' modulation, a condition in which the phase of one pair of diagonally opposing inducers was shifted by a quarter of a cycle, rather than half a cycle as in the antiphase condition. With antiphase modulation, the luminances of the inducers are asynchronous, but the instants of contrast reversal remain synchronous. Synchronous contrast reversal, even if opposite in phase, may facilitate grouping under some circumstances (Lee & Blake, 1999).

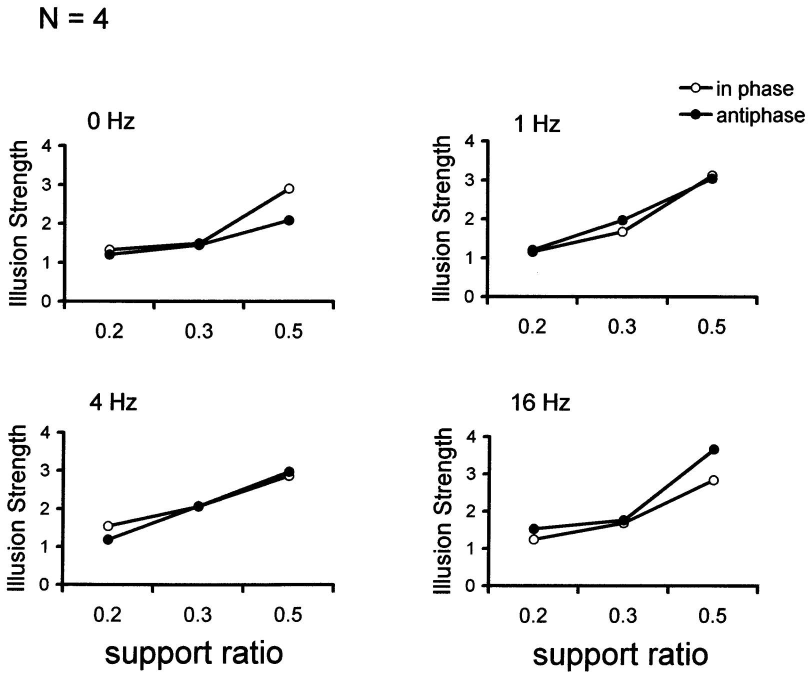

Fig. 2. Illusion strength $S = (\ln r_{out})/(\ln r_{in})$ at a range of support ratios, for inducers in phase (open symbols) or antiphase (solid symbols), at four flicker frequencies. Geometric means across four subjects.

But with quadrature phase modulation, the instants of contrast reversal are maximally separated in time. This quadrature phase condition also has an anomalously large effect on vernier acuity thresholds (Victor & Conte, 1999). At a flicker frequency of 4 Hz, the log aspect ratio thresholds ($\ln r_{in}$, $\ln r_{out}$) and their ratio $S = \ln r_{out}/\ln r_{in}$ for the quadrature phase conditions (data not shown) were not statistically different from their values in the in phase and antiphase conditions ($P > 0.1$ within each of three subjects for both $\ln r_{in}$ and $\ln r_{out}$ by unpaired t-test, $P > 0.2$ across subjects for S by paired t-test).

3.2. Experiment 2: dependence on support ratio

To rule out the possibility that our measure S was insensitive to a graded change in illusory contour strength, we examined the dependence of S on support ratio (Fig. 2). At a support ratio of 0.2, S was close to 1, and, as in the data of Fig. 1C, S was in the range 2.5–3 at a support ratio of 0.5. For the intermediate support ratio 0.3, intermediate values of S (1.5–2) were obtained, both in the group means as illustrated, and in the data from each subject. The slight decrease in illusion strength for the antiphase condition at 0 Hz with a support ratio of 0.5 reproduces the findings in Fig. 1. At 16 Hz, there was an increase in illusion strength $S = \ln r_{out}/\ln r_{in}$ for the antiphase condition, and reflected the behavior of a single subject (LC), who showed both a modest decrease in r_{in} and a comparable increase in r_{out} under these conditions. Across the 12 conditions (four frequencies, three support ratios), none of the differences between the in phase and antiphase conditions were statistically significant ($P > 0.05$). In sum, Fig. 2 demonstrates that our assay provides a graded measure of illusory contour strength and that gradations in strength do exist, but (within the parameter range we studied), these gradations do not depend on the relative phase of the inducers.

3.3. Experiment 3: dependence on perceptual organization

Previous studies (Matthews & Welch, 1997; Spehar, 1998; He & Ooi, 1998a,b), found perceptual differences of illusory contours that depended on the polarity of the inducers. These studies differed from ours both in the design of the stimuli and in the approach to assay illusory contour strength (magnitude estimation or search reaction time). We next examined whether differences in stimuli might account for the differences in results.

Fig. 3A and B demonstrate the effects of altering the standard Kanizsa square along the lines suggested by the 'Illusory O' of He & Ooi (1998a,b). As demonstrated by these authors, if the wedges are of matching polarity to their associated inducers, amodal completion of an occluding square frame is facilitated (Fig. 3A), whether adjacent inducers are in phase or in antiphase. If the wedges and the associated inducers are of opposite polarity (Fig. 3B, 'mismatch' conditions), amodal completion of the occluding square is reduced. The corresponding scene interpretation of occluded but non-uniform disks would require a non-generic scene interpretation (Nakayama & Shimojo, 1992) in which the occluder 'accidentally' occludes just the portion of the disks in which luminance contrast changed. However, despite this difference in perceptual organization, we found no difference between aspect ratio thresholds r_{in} in these four conditions, for either static or flickering (1, 4, and 16 Hz) conditions ($P > 0.05$).

Spehar (1998, 1999) demonstrated that shape discrimination of a closed contour was impaired when contrast reversals occurred along its edges, but not when these reversals occurred at the corners. To determine whether such reversals had an effect on our assay of contour strength, we modified the stimuli as shown in Fig. 3C. We used sector angles of 120 and 150 deg, rather than 135 deg, lest the alignment of the partitions along the diagonal provide another cue to aspect ratio. In phase and antiphase configurations both had contrast reversals at the corners, but only the in phase configuration had a contrast reversal along the illusory edge. Thus, according to Spehar's results, perceptual closure of the squares might be facilitated in the antiphase condition. However, as seen in Fig. 3C, threshold log aspect ratios $\ln r_{in}$ were unaffected ($P > 0.05$) by relative phase, and very similar to those measured in other configurations with a support ratio of 0.5 (Fig. 1B, Fig. 2 and Fig. 3A and B).

3.4. Experiment 4: spatial separation and dynamics in a vernier task

The final experiment examines the effect of a gap between stimulus components in a vernier alignment task for which there is a striking effect of relative phase when no gap is present (Victor & Conte, 1999). Bar stimuli (0.5×0.125 deg) were modulated at 2 Hz, near the peak of the phase effect previously reported for abutting bars (gap of 0 deg). The effects of this manipulation are shown in Fig. 4 at two contrasts, for an individual subject (Fig. 4A) and a mean of three subjects (Fig. 4B). In the no-gap condition, we reproduced our previous findings of an approximately threefold improvement in vernier thresholds in the in phase condition, compared with the threshold in the antiphase

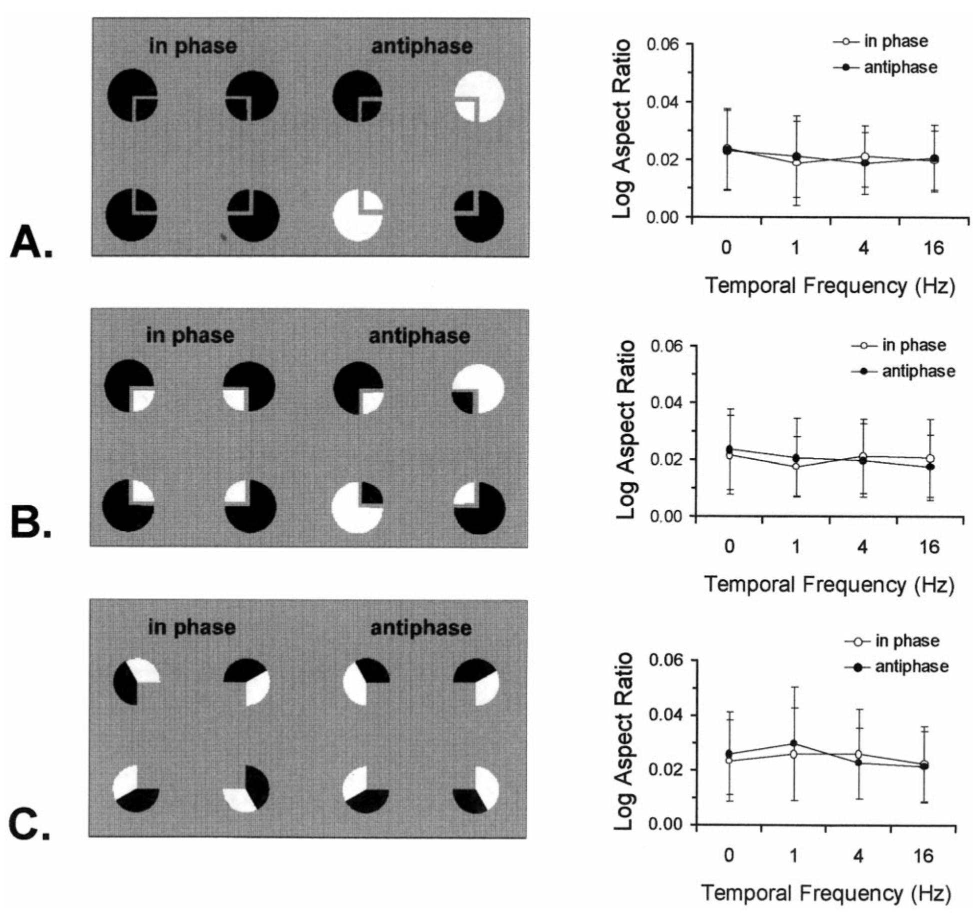

Fig. 3. Mean threshold log aspect ratios $\ln r_{in}$ for shape discrimination of illusory squares, with inducers modified by an additional wedge that is matched (A) or mismatched (B) in contrast polarity. Panel C, mean threshold log aspect ratios $\ln r_{in}$ with inducers modified by contrast reversal across an internal contour. In each case, inducers were presented in phase (left diagrammed stimulus, open circles) and antiphase (right diagrammed stimulus, filled circles). Error bars as in Fig. 1B. $N = 5$ (A, B); $N = 6$ (C).

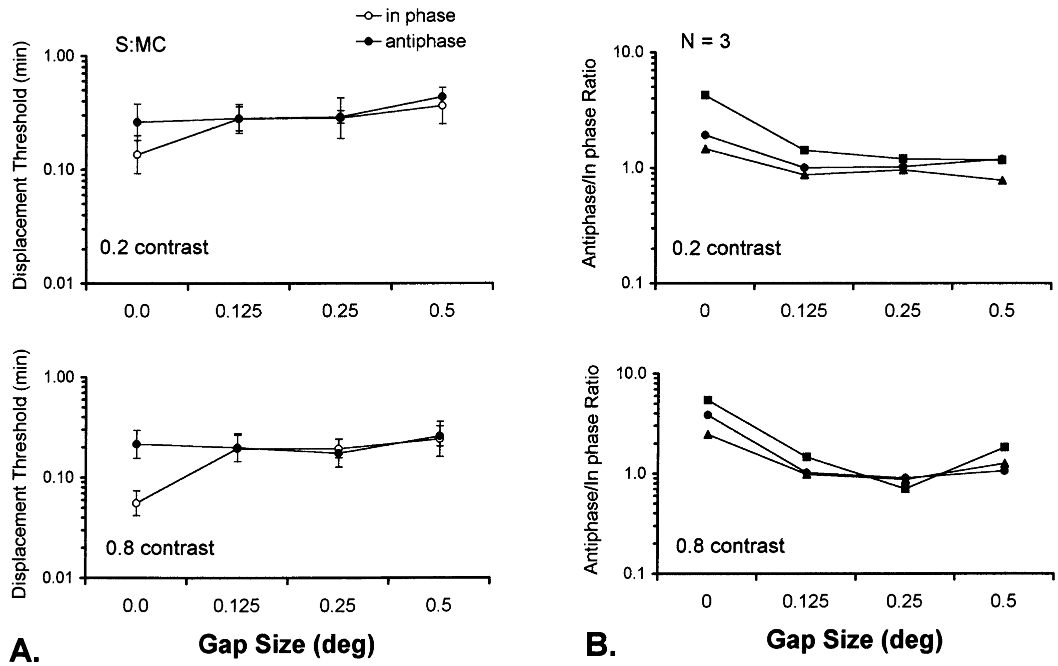

Fig. 4. Dependence of displacement threshold on gap size. Vernier bars were 0.5 × 0.125 deg, and flickered at 2 Hz. (A) Displacement thresholds for bars presented in phase (open circles) and antiphase (filled circles), at two contrasts. Error bars in Panel A represent ± 2 S.E.M., calculated from the subject's repeated staircase determinations for each condition. Subject MC. (B) Ratios of displacement threshold (antiphase/in phase) for three subjects. Data from the subject of panel A are plotted with circles.

condition. This improvement is comparable to the improvement seen for static stimuli (Mather & Morgan, 1986; Levi & Westheimer, 1987; O'Shea & Mitchell, 1990). But with even a small gap (0.125 deg in this subject), the difference between in phase and antiphase presentation is lost. The effect of the gap was to elevate the threshold for the in phase condition, rather than to decrease the threshold for the antiphase condition. This is consistent with the notion that there is a special mechanism recruited for the abutting vernier task in the in phase condition, but not with the notion that antiphase presentation interferes with judgment of alignment. Small gaps sufficed to equate the thresholds for the in phase and the antiphase condition, a gap of 0.125 deg in two subjects, and a gap of 0.25 deg in the third subject (Fig. 4B). These findings were consistent across contrasts ($c = 0.2$ and $c = 0.8$, as shown).

Similar results were found for stimuli scaled up by a factor of two (1.0 × 0.25 deg bars with 0.25 deg gap) and four (2.0 × 0.5 deg bars with 0.5 deg gap) in spatial extent. All threshold ratios (antiphase/in phase) were not significantly different from 1 via paired t-tests. Thus, the loss of sensitivity to relative phase seen with the larger gaps depends on the absolute size of the gap, rather than its size relative to the bar.

4. Discussion

4.1. Summary of results and comparison with previous studies

We used a quantitative and demonstrably graded (Fig. 2) measure of illusory contour strength to look for effects of the relative phase of inducers on the strength of the illusory contours that define a Kanizsa square. We found no effect of phase on the strength of the illusory contours over a range of flicker frequencies from 1 to 16 Hz, either with standard Kanizsa squares (Figs. 1 and 2) or with modifications designed to alter the ways in which the illusory squares could be perceived (Fig. 3). For flickering inducers, these findings extend a previous study of the effects of inducer asynchrony (Fahle & Koch, 1995) to a lower frequency range. For static inducers of opposite polarity, an illusory contour is present (Shapley & Gordon, 1983, 1985, 1987; Grossberg & Mingolla, 1985), but our quantitative measures show that it is reduced in strength, consistent with recent studies based on a formal rating scale or saliency in a search task (Matthews & Welch, 1997; He & Ooi, 1998a,b; Spehar, 1998, 1999).

He and Ooi (1998a,b) suggest that the illusory contour percept is related to a perceptual organization of the Kanizsa square stimulus into two depth planes, with the illusory square seen as an opaque object that partially occludes four disks. The completion of the illusory square is considered to be 'amodal', since it does not differ from the background along any modality. A similar interpretation of other novel illusory contours was recently advanced by Williams and Rubin (1998). This amodal completion of the contour between inducers (for example Figure 2 and Figure 3 of He & Ooi, (1998b) and our Fig. 1) would account for a lack of dependence of the contour strength on inducer polarity, since the occluding square would be just as vivid, whether it occluded like-contrast disks (in phase condition) or opposite-contrast disks (antiphase condition). In further support of this notion, He and Ooi (1998a,b) introduced variations of the Kanizsa square (the 'Illusory O'), in which inducer polarity influenced whether scene organization was consistent with an unseen occluding object (Figure 4 of He & Ooi (1998b)). Under static conditions, their rating-scale measures indicated a strong dependence of the strength of the illusory contours on the contrast polarity of the inducers.

Our findings differ, in that we found no difference in illusory contour strength for comparable variations of the Kanizsa square, either under static conditions, or when the inducers were modulated in antiphase. While there is an apparent subjective difference in the saliency of the squares due to these manipulations, there is no degradation in shape discrimination (Fig. 3A and B). As shown in Fig. 2, if there were a difference in illusion strength comparable to a 25% reduction of the support ratio, then our procedures would have been able to detect it. In the rating-scale approach, the basis for the subjects' judgments is uncertain — but it is reasonable that the judgment criterion is shaped by the stimuli used for training: exemplars in which the inducers are in phase. Another possibility is that subjects made use of an induced brightness illusion across the illusory contour (Dresp & Bonnet, 1991). An illusory brightness difference would have been ambiguous or eliminated (Dresp, Salvano-Pardieu, & Bonnet, 1996) in the antiphase (opposite-polarity) condition. The most interesting possibility for the discrepancy in results is that there is a distinction between a low-level process that extracts contours, and a higher-level process that extracts scene organization (Nakayama & Shimojo, 1992). This is suggested both by inspection of the examples in Fig. 3 and the interpretation of He and Ooi (1998b), and would account for the absence of polarity effects in our task but not in those that are weighted by overall scene organization (He & Ooi, 1998a,b; Spehar, 1998, 1999).

The task we used relies on neither the use of exemplars nor perceived brightness differences, but just on the finding (Regan & Hamstra, 1992) that aspect ratio discrimination for a rectangular object is several fold better than discrimination of relative distances of isolated pairs of points. The ability to perceive small changes in the geometry of the illusory object requires the presence of the illusory contours for two-dimensional (Rubin, Shapley, & Nakayama, 1995; Ringach & Shapley, 1996) and three-dimensional (Carman & Welch, 1992) curvature judgments. We suspect that had we used one of these other shape tasks (for example, by comparing thresholds for thin vs. thick judgments Rubin et al. (1995) as a function of relative phase), the results would have been similar to what we found with the aspect ratio task.

4.2. Comparison with vernier alignment

Vernier judgments and illusory contour formation are both early stages of visual analysis in which elementary stimulus components are processed jointly, and the extent to which these components are grouped is strongly dependent on their relative geometry. As such, both processes represent an early stage of the 'binding' of stimulus components into a composite (Fahle & Koch, 1995), i.e. object extraction. The lack of dependence of illusory contour strength on relative contrast polarity or phase of the inducers differs from the well-known characteristics of vernier alignment. Vernier alignment thresholds for static stimuli are several times lower for stimulus components of like contrast polarity (Mather & Morgan, 1986; Levi & Westheimer, 1987; O'Shea & Mitchell, 1990), and alignment thresholds for flickering stimuli are two to three times lower for stimuli whose components are in phase than for stimuli whose components are out of phase (Victor & Conte, 1999).

Illusory contour formation and vernier acuity share a precise dependence on spatial arrangement, but there are also obvious differences between these two processes. Vernier acuity can be demonstrated with stimuli that are nearly confined to a single orientation, but illusory contour stimuli necessarily involve the interaction of two (or more) orientations. Although introduction of spatial offsets generally interferes markedly with the strength of the illusory contour (Fahle & Koch, 1995), other spatial manipulations have modulatory effects — such as altering the perceived curvature and three-dimensional structure of a surface (Carman & Welch, 1992) or its brightness (Grossberg & Mingolla, 1985). Illusory contour formation has been shown to be affected by 'top–down' influences of scene organization (Lesher & Mingolla, 1993; Ramachandran, Ruskin, Cobb, Rogers-Ramachandran, & Tyler, 1994; He & Ooi, 1998a,b; Spehar, 1998, 1999).

Nevertheless, it appears that separation of the stimulus components, rather than these other factors, underlies the differential effect of relative phase in these two tasks. As shown in Fig. 4, insertion of a small gap into the vernier stimulus eliminates the effect of relative phase. The Kanizsa square configuration is incompatible with the converse experiment, since eliminating the gap (support ratio equal to 1) replaces the space for the illusory contour by a real contour. Moreover, our approach cannot be used for support ratios close to 1, since the length of the gap would be a strong confound in the shape judgment task. Thus, we cannot directly determine whether closing the gap will allow for the emergence of temporal effects. However, experiments based on another illusory contour stimulus, offset gratings, have shown a contrast polarity effect for abutting stimuli (Dresp et al., 1996).

By demonstrating a common pattern of dependence on relative temporal phase and separation, our analysis expands the relevance of the short-range versus long-range dichotomy that characterizes performance in vernier and other (Levi, Jiang, & Klein, 1990) hyperacuity tasks (reviewed in Victor & Conte, 1999) to tasks involving extended contours (Dresp, 1999; Dresp & Grossberg, 1997). In the short-range regime (Klein & Levi, 1985; Wilson, 1986), contrast and temporal effects on vernier and related tasks are prominent, consistent with the notion that tuning properties of individual neurons with quasilinear receptive fields play a limiting role in performance (Shapley & Victor, 1986; Swindale, 1995). In the long-range regime, contrast and temporal effects are weak or absent, and performance appears to be limited by positional uncertainty (Burbeck, 1987; Morgan, Ward, & Hole, 1990; Kooi, DeValois, & Switkes, 1991; Levi & Waugh, 1996) of tokens extracted at an earlier stage of processing. The stage of token extraction is presumably mediated by neurons that can be modeled in a quasilinear fashion, followed by a local non linearity. The second stage of analysis, at which these tokens are jointly analyzed, follows the local non linearity (Levi & Waugh, 1996), and thus is insensitive to the internal detail of the tokens, including temporal composition as shown here, and spatial frequency composition (Dakin & Hess, 1998). Successful computational models for illusory contours (Heitger, Rosenthaler, von der Heydt, Peterhans, & Kubler, 1992; Gove, Grossberg, & Mingolla, 1995) and related grouping phenomena (Gove et al., 1995Grossberg, Mingolla, & Ross, 1997; Yen & Finkel, 1998) share these main features of local feature extraction (requiring a local non-linearity) followed by a long-range (also non-linear) interaction. Moreover, this picture is consistent with the major architectural features of V1 and V2 (Spitzer & Hochstein, 1985; Ts'o, Gilbert, & Wiesel, 1986Heitger et al., 1992 Gilbert, Das, Ito, Kapadia, & Westheimer, 1996).

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