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Grouping and segmentation in binocular rivalry ☆

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Abstract

Dichoptic presentation of dot arrays produces binocular rivalry if the arrays are of opposite contrast relative to background. Rivalry can occur even if individual dots in one eye's array do not overlap with the dots in the contralateral eye's array. The amount of unitary perception of only one array is a measure of the probability that the stimuli rival as textured surfaces rather than as portions of arrays or as individual dot elements. In accordance with Gestalt grouping principles, arrays of uniform brightness or color produced more unitary perception than mixed arrays. However, experiments with parametric variation of dot motion coherence suggested that segmentation mechanisms based on detection of collinearity can also influence perceptual selection and suppression in binocular rivalry.
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1. Introduction

Binocular rivalry is a form of multistable perception that occurs when each of the two eyes is presented with visual stimuli that are different from each other and cannot be fused into a single coherent percept. Under these circumstances, the percept typically alternates between two states corresponding to the left eye's stimulus and the right eye's stimulus or between two gestalts that are formed by combining parts of the monocular stimuli (Diaz-Caneja, 1928). The percepts generated by rivalrous stimuli provide insight into the nature of the representations of these stimuli. Therefore, in addition to being a fascinating phenomenon in its own right, binocular rivalry can be used to study mechanisms of perceptual selection and suppression (Alais & Blake, 1999; Blake & Logothetis, 2002; Bonneh, Sagi, & Karni, 2001; Leopold & Logothetis, 1999).

In the present study, we employed rivalrous stimuli consisting of arrays of dots of opposite contrast relative to background luminance (Fig. 1A). These arrays have

the same dot spacing in the two eyes, but the two arrays are spatially offset with respect to each other. Specifically, the retinotopic location of a single dot in one eye is equidistant from the locations of the nearest dots in the other eye's stimulus (Leopold, 1997; Logothetis, 1998). Thus, although the arrays are overlapping in visual space, the individual dots do not overlap. If the competition underlying binocular rivalry occurred only at the level of the individual dot elements, the percept of these stimuli would be a fusion of the two arrays, and every dot would be visible (Fig. 1B). However, the percept of fusion does not generally occur for these dot arrays except for dot spacings of approximately 1 deg of visual angle or greater (Leopold, 1997; Logothetis, 1998). For arrays with dot spacings of less than 1 deg, two different types of percepts are generally reported. The first is a piecemeal rivalry in which complementary regions of each array dominate over the corresponding regions in the other stimulus (Fig. 1C). The second is a unitary percept in which an entire array is seen while the other array is phenomenally suppressed (Fig. 1D and E). The probability of such unitary percepts would be vanishingly small if binocular rivalry were the result of independent competition between small retinotopic zones (Kovács, Papathomas, Yang, & Fehér, 1996). The existence of any unitary perception of these arrays suggests that the dots are grouped together and that the stimuli can compete at a more global level as textured

STIMULI

left eye   right eye

POSSIBLE PERCEPTS

binocular fusion   piecemeal rivalry

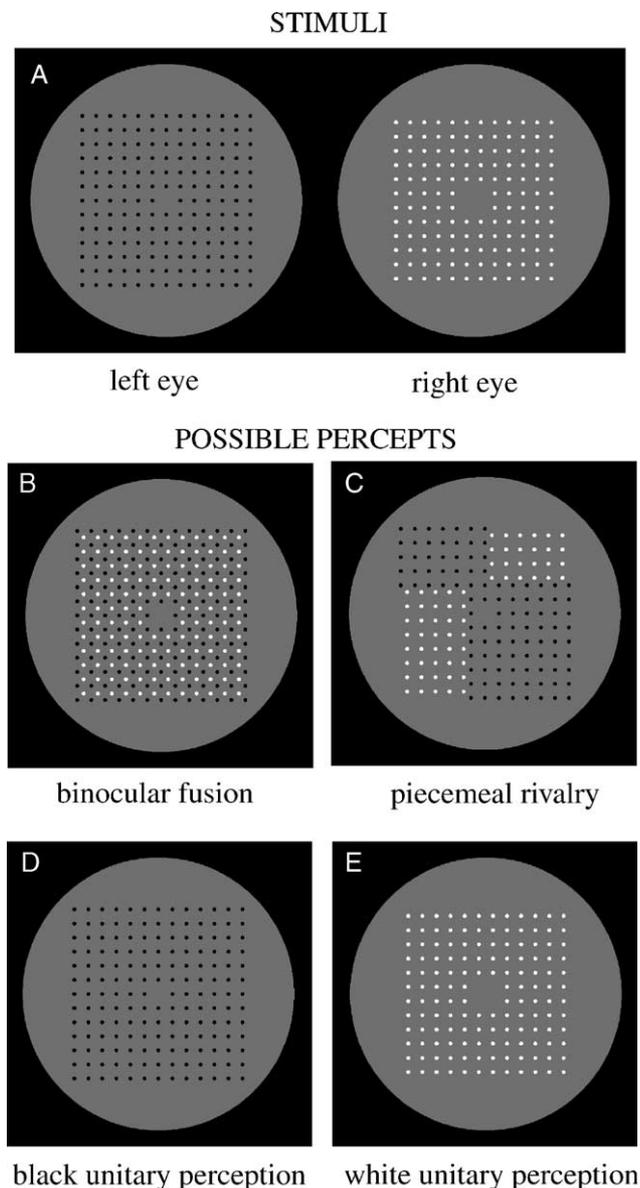black unitary perception   white unitary perception

Fig. 1. Visual stimuli and schematic diagrams of possible percepts. (A) Rivalrous dot arrays in which the arrays overlap in visual space but the individual dot elements do not. In this example, the size of the array presented to the left eye subtended 8×8 deg of visual angle, and the distance between dot boundaries in the two eyes was 0.28 deg. Additional binocular vergence cues to stabilize eye position are not shown. These included fixation points in the centers of the arrays and lines flanking all four sides of the arrays (see Section 2.2). (B) Binocular fusion of the two arrays. This percept would be expected if competition occurred at the level of individual and independent dot elements. In this case, because the individual dots do not overlap, they are all simultaneously visible. (C) Piecemeal rivalry. (D, E) Unitary perception of only one array with complete phenomenal suppression of the other array, indicating competition between textured surfaces instead of competition between individual dot elements.

surfaces. This is consistent with the finding that rivalrous dot arrays containing random mixtures of black and white dots in each eye can generate percepts that are predominantly one color or the other, indicating inter-

ocular grouping of dots that have the same luminance (Leopold, 1997).

We have manipulated the composition of rivalrous dot arrays to test the roles of classical Gestalt principles of grouping by brightness, color, or common fate (coherent motion) in the conscious perception of these stimuli. Each pair of dot arrays contained a test stimulus presented to one eye and a fixed reference stimulus presented to the other eye. Changes in stimulus composition (brightness, color, or motion coherence) always occurred in the test stimulus and not in the contralateral reference array. The tendency of the arrays to compete as textured surfaces was quantified by measuring the percentage of viewing time in which a unitary percept of either the test or reference array occurred. Our results demonstrate grouping by common luminance and color. However, for arrays of moving dots, coherent motion produced less unitary perception than incoherent motion, in contradiction to the Gestalt principle of grouping based on common fate. We propose that the moving collinearities in dot arrays with coherent motion activate segmentation mechanisms that disrupt unitary perception and prevent grouping based on common fate.

Finally, all of the grouping and segmentation effects we observed were due to changes in unitary perception of the test array. In no case did alterations in the composition of the test array result in changes in the amount of unitary perception of the contralateral reference array. This pattern of results differs from previous studies in which changes in stimulus strength (luminance (Fox & Rasche, 1969); contrast (Levelt, 1968); velocity of motion (Bossink, Stalmeier, & de Weert, 1993)) in one stimulus altered the mean duration of dominance of the unchanged contralateral stimulus. Thus, the effects of grouping and segmentation on binocular rivalry are distinct from the effects due to changes in stimulus strength.

2. Methods

2.1. Subjects

A total of 15 paid volunteers participated in this study. All had normal or corrected-to-normal vision and were screened for deficits in stereoscopic or color vision. None of them had knowledge about the experimental hypotheses or about binocular rivalry in general.

2.2. Stimuli

Subjects viewed arrays of dots through a custom-built stereoscope that allowed images on two monitors to be independently presented to the two eyes. The gamma-corrected monitors had a pixel resolution of 1280×800 pixels and a frame refresh rate of 90 Hz. The viewing

distance was 123 cm. One of the stimuli was a 12×12 dot array that subtended 7.3×7.3 deg of visual angle, resulting in a dot spacing of 0.65 deg (center to center; distance between boundaries of adjacent dots was 0.47 deg; Fig. 1A, ''right eye''). Each dot had a diameter of 0.18 deg and a circular shape (except for the experiments involving moving dots, in which each dot was a 0.18×0.18 deg square). The array presented to the other eye had the same dot spacing, but the dots were positioned so that there was no overlap between dots in the two arrays. If the two arrays were overlaid (as in Fig. 1B), a given dot in one array would be equidistant from the surrounding dots in the other eye. To accomplish this, it was necessary to make one of the arrays slightly larger than the other. The larger stimulus was a 13×13 dot array and subtended 8.0×8.0 deg (Fig. 1B, ''left eye''). When the two arrays were overlaid, the interocular distance (the distance between the boundaries of one eye's dots and the boundaries of the other eye's dots) was 0.28 deg. Because the larger array had a slight advantage over the smaller array in binocular rivalry, the two array sizes were always counterbalanced across all experimental conditions and across both eyes.

In addition to the arrays, vergence cues were presented to minimize non-conjugate eye movements. The arrays were presented on a neutral gray background within a circle 12.5 deg in diameter. The inside of the stereoscope was very dark, and the subjects could see only the visual stimuli; the monitor frames and mirrors were not visible. Therefore, the circles bounding the stimuli served to align and stabilize the positions of the eyes. In addition, four flanking yellow lines were binocularly presented, one on each side of the square array. These were parallel to the outer boundary of the arrays and were 0.18×6.3 deg in size. They were presented 4.9 deg from the fixation point, corresponding to a distance of 0.84 deg from the inner boundary of the line to the outer boundaries of the dots making up the larger of the two dot arrays. Finally, a circular colored fixation point (blue for color experiments, red for all other experiments) 0.18 deg in diameter was presented to both eyes. Because the fixation points were binocularly fused, they could have disrupted rivalry in the surrounding dots. To prevent this, no rivalrous dots were presented less than one dot spacing (0.65 deg) from the fixation point.

The exact composition of the dot arrays depended upon the experiment. For luminance experiments, one array (the reference array) consisted of light gray dots with luminance 35.8 cd/m². The array presented to the other (the test array) contained either dark gray (7.6 cd/m²), black dots (luminance too low to accurately measure), or a combination of the two. The luminance values were chosen so that, on average, the two arrays had approximately equal contrast relative to the background luminance of 19.3 cd/m². The proportions of dark gray dots were 0%, 5%, 10%, 25%, 40%, 60%, 75%, 90%, 95%, and 100%.

These ten conditions were counterbalanced across both eyes and array types (larger and smaller, see above), resulting in a total of 40 trials.

For color experiments, one array contained light gray dots (31.5 cd/m²), and the other was made up of red dots, green dots, or a combination of red and green dots. The perceived luminances of the red and green dots were equated using a modification of the classic heterochromatic flicker technique. Subjects binocularly viewed a 1.8×1.8 deg red square flickering at 22.5 Hz on a background of luminance of 7.6 cd/m². They continuously adjusted the luminance of the square to minimize the perception of flicker. This was repeated ten times, and the average of the ten luminance measurements was used for the red dots in the color rivalry experiments. The procedure was repeated with a green square. This resulted in red and green luminances in the rivalry experiments that were equal to each other and also had the same perceived contrast as the rival array of light gray dots (relative to the neutral gray background). As in the luminance experiments, there were 10 proportions of red and green dots, and these were counterbalanced across eyes and array types (larger and smaller) to produce 40 trials in total.

The motion experiments contained a static array of square dots in one eye and a moving array presented to the other eye. One eye viewed black dots (luminance too low to accurately measure) and the other viewed white dots (luminance of 39.9 cd/m²). For dynamic jitter, concentric motion, and uniform phase motion, there were six levels of motion coherence: 0%, 10%, 35%, 65%, 90%, and 100% coherence. In addition, there was a condition of static versus static. These seven conditions were counterbalanced across eyes, across array types (larger and smaller), and black/white (either black moved and white was stationary or vice versa), resulting in 56 trials. For the experiments with coherent row or column motion, there were five conditions: 100% coherence, coherently moving columns, coherently moving rows, 100% incoherence, and static. These five test conditions were always rivaling against a static reference array, and they were counterbalanced across eyes, array types, and black/white, resulting in a total of 40 trials.

The dynamic jitter motion (Movie 1) consisted of a 0.045 deg displacement of each dot from the starting position over a time period of 55.6 ms (5 monitor refresh frames), resulting in a speed of 0.8 deg/s. The dots immediately returned to the starting point along the same path and with the same velocity. This cycle of displacement and return was repeated for the duration of the trial (60 s), and each displacement had a different and random angle of motion. For coherent motion, the angles and phases of motion were the same for all of the dots. For incoherent motion, the angles and phases were randomized. Thus, the motion of an individual dot in a

coherently moving array was indistinguishable from the motion of a dot in an array with completely incoherent motion. The difference between coherent and incoherent motion was only in the relative phases and angles of motion of the individual dots. For uniform phase motion (Movie 3), the characteristics of the motion were the same as that of dynamic jitter, except that in the case of incoherent uniform phase motion, only the angles of motion were randomized, not the phases. Coherent concentric motion (Movie 2) consisted of oscillations along trajectories emanating from the fixation point. The displacement from the starting point (either towards or away from the fixation point) was again 0.045 deg, and the speed was 0.8 deg/s.

The experiments involving coherent motion of rows or columns (Movie 4) had constant angles of motion across all conditions. One experimental session used motion along a diagonal rotated 45 deg clockwise relative to vertical, while the other used motion along a diagonal rotated 45 deg counterclockwise relative to vertical. The dots oscillated at a speed of 0.8 deg/s along the diagonal with a displacement from the starting point of 0.045 deg. For these stimuli, the angles of motion were constant across all conditions; only the phases of motion varied (complete coherence, coherently moving columns, coherently moving rows, or complete incoherence). Examples of all the motion stimuli employed in this study can be viewed at socrates.berkeley.edu/~masilver/dotsurf

2.3. Procedure

Before data collection, subjects ran at least one practice session of approximately one hour to familiarize themselves with the stereoscope and the task. Trials consisted of one minute of continuous stimulus presentation, and responses were made using a button box. For most of the experiments, subjects were instructed to press one button when they perceived only white dots with no black dots and to press the other button when they perceived only black dots with no white dots. The buttons were held down for the entire duration of the unitary percept. Subjects were told to withhold button presses when they saw white and black dots simultaneously. For the luminance experiments, the instructions were to report unitary perceptions of dark (darker than background) or light (lighter than background) rather than white and black. Similarly, for the color experiments, unitary perceptions of color or white were reported. Because we were interested in the effects of stimulus changes on the amount of unitary perception, we excluded 2 subjects who had such an extreme response bias that their percentages of unitary perception for the stimuli shown in Fig. 1A were 0% and 0.09%.

Very occasionally, both buttons would be simultaneously held down. These events were always immediately preceded by a period in which one button was held down and immediately followed by a period in which the other button was held down, and the duration of these events was usually a few hundred milliseconds or less. Presumably in these cases the subject experienced an instantaneous transition from one unitary percept to the other. These intervals were treated as if they contained piecemeal rivalry, because it was unclear which unitary percept corresponded to the interval during which both buttons were being simultaneously pressed. This correction resulted in a very small underestimate of the percentages of unitary perception and of the average durations of unitary percept.

Subjects were instructed to maintain fixation for the duration of the trial, although this was not verified by measurements of eye position. The intertrial interval was typically about 15 s, but for the motion experiments it was somewhat longer (20–30 s) because an animation of moving dots was loaded from disk before every trial. Subjects could pause the experiment between trials and resume whenever they wanted to.

For each stimulus, the data were expressed as unitary perception (the percentage of viewing time during which the corresponding button was held down), frequency of button presses, and average duration of button presses. Variations in stimulus composition were only made for the test array, while the contralateral reference array remained constant. Unitary perception data were collected for both the reference and test arrays for every condition. The intersubject variability for baseline values for these measures was relatively high (see Section 3.2). Therefore, all data were normalized to a control condition for each session. For luminance, the control conditions were all dark gray or all black. Data from conditions of 95% dark gray/5% black, 90%/10%, 75%/25%, and 60%/40% were all normalized with respect to 100% dark gray using the following contrast index:

Unitary perception index

$$= \frac{(\text{mixed stimulus} - \text{uniform stimulus})}{(\text{mixed stimulus} + \text{uniform stimulus})}$$

Similarly, data from 40% dark gray/60% black, 25%/75%, 10%/90%, and 5%/95% were normalized with respect to the uniform black condition. This allowed all data to be combined and expressed as a contrast index relative to uniform luminance, with percentage of dots of secondary brightness as the independent variable. Separate unitary perception indices were computed for the test array and for the contralateral reference array for each condition. A similar procedure was used to compare uniform and mixed color (percentage of dots of secondary color), motion (percent motion coherence; normalized to 100% motion coherence), and coherently moving rows or columns (100% coherence, coherent

rows or columns, and 0% coherence; normalized to stationary arrays).

3. Results

3.1. Competition between textured surfaces

Subjects were presented with rivalrous dot arrays of opposite contrast with respect to background. The stimuli were shown for 60 s, and the subjects were instructed to press one button if they experienced unitary perception of one stimulus (for example, a percept of all white dots and no black dots) or a second button if they experienced unitary perception of the other stimulus. They held the buttons down for the entire duration of the unitary percepts.

The existence of any unitary perception of these arrays indicates that competition can occur at the level of textured surfaces (Leopold, 1997; Logothetis, 1998). The unitary percept, by definition, is complete dominance of one array and complete suppression of the other. We tested whether the end of a period of unitary perception (release of one of the arrays from suppression) also occurred as a result of competition between surfaces. In principle, a unitary percept could result from at least two types of processes. The first possibility is that the default perceptual state is a mixed percept combining elements or regions from both arrays, and occasionally the dots from one array are grouped to form a unitary percept. At the end of the period of unitary perception, the grouping would disintegrate, and the percept would revert to the default mixed state. The second possibility is that the two arrays can compete as surfaces throughout periods of unitary perception. In this case, the end of a period of unitary perception of one array would be more likely to be followed by unitary perception of the other array as it undergoes a transition from suppression to dominance.

To discriminate between these two models, we measured the intervals between the end of one period of unitary perception and the beginning of the next, and we divided the measurements into two categories: (1) unitary perception of one array followed by unitary perception of the same array and (2) unitary perception of one array followed by unitary perception of the other array. The results are shown in Fig. 2. The distributions of the intervals for these two events indicate that there was a large population of very brief intervals (<500 ms) that occurred only for switching of unitary perception from one array to the other. This population was not present for unitary percepts of one array followed by another period of unitary perception of the same array. Given that the subjects had to release one button to signal the end of each period of unitary perception and press another button to indicate the beginning of the
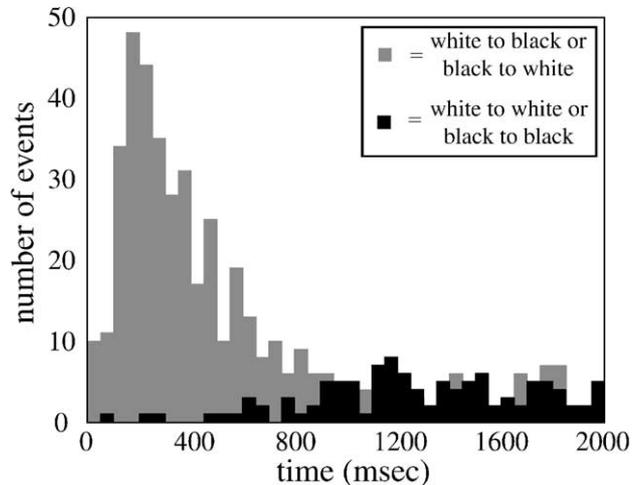

Fig. 2. Arrays can be released from perceptual suppression as surfaces. The durations of intervals between the end of one period of unitary perception and the beginning of the next unitary perception were plotted as a histogram. *Gray* indicates a period of unitary perception of one array followed by unitary perception of the competing array, while *black* is unitary perception of one array with subsequent unitary perception of the same array. There are many more short duration events (<500 ms) in the gray histogram, indicating that after termination of a period of unitary perception, the visual system does not return to a default state of a mixed percept. Rather, the previously suppressed array, after being released from suppression, often immediately dominated perception and completely suppressed the array that was previously dominant. These data are pooled from 20 experiments from 10 subjects.

next unitary percept, an interval of 500 ms or less signifies practically instantaneous switching of unitary perception from one stimulus to the other.

Although only those intervals with durations between 0 and 2000 ms are shown in Fig. 2, the overall populations of the two types of events are also quite different. For unitary percepts of one stimulus followed by unitary percepts of the other, the median interval was 553 ms. For unitary perception of one stimulus followed by unitary perception of the same stimulus, the median interval was 3050 ms. There were also more total events involving unitary percepts of one stimulus followed by the other (589) than unitary percepts of one stimulus followed by unitary perception of the same stimulus (336). These results indicate that release of an array from suppression is likely to be immediately followed by unitary perception (dominance) of that array. Thus, during periods of unitary perception, both the dominant and suppressed arrays are likely to be competing with each other as textured surfaces.

3.2. Grouping based on common luminance

For the stimuli shown in Fig. 1A, the percentage of viewing time in which a unitary percept occurred was $10.7 \pm 10.4\%$ (s.d., $n = 24$ experimental sessions from 12 subjects, range 0–44.3%). However, repeated

experiments with the same subjects indicated that the response criteria of individual subjects were consistent across experimental days. The absolute value of the difference in percent unitary perception on two separate days was $3.7 \pm 4.3\%$ (s.d., $n = 12$ subjects). Much of the large intersubject variability is attributable to the fact that, for this task, no feedback was available to the subjects to standardize their response criteria. There was no objectively correct answer concerning how much unitary perception a subject should experience, and the subjects' responses reflect individual differences in response criterion. The intersubject variability could be greatly reduced by normalizing the data for each subject. Most of the experiments in this study involve rivalry between a test array that varies along some stimulus dimension (for example, motion coherence) and a fixed reference array presented to the other eye. In principle, changes in the test array could affect unitary perception of the test array itself and/or unitary perception of the unchanged contralateral reference array. Raw percent unitary perception data were collected for both the test and reference array for each stimulus condition and then normalized and expressed using the following contrast index:

Unitary perception index

$$= \frac{(\text{mixed stimulus} - \text{uniform stimulus})}{(\text{mixed stimulus} + \text{uniform stimulus})}$$

The individual terms in the contrast index are percentages of viewing time in which a unitary percept occurred. The unitary perception index allows relative unitary perception values to be computed for each subject and each condition by comparing a mixed test array condition (for example, a stimulus containing red and green dots rivaling with a gray reference array) to a uniform test array condition (a stimulus containing either all red or all green dots rivaling with the reference array). The proportions of red and green dots varied only in the test stimulus, while the contralateral reference stimulus remained constant. The unitary perception index is a means of comparing across stimulus conditions (mixed versus uniform), and it does not directly relate levels of unitary perception for the test array and the contralateral reference array (see Section 2.3). In fact, the test array and the contralateral reference array each generate their own value of the unitary perception index for each stimulus condition.

We first applied this unitary perception index to study the effects of grouping by common brightness. One eye was shown a reference array that contained dots brighter than the background, and this array was held constant across all conditions. The other eye viewed one of three types of array, all of which contained dots that were darker than the background: uniform dark gray dots, uniform black dots, or a mixture of dark gray and black dots (Fig. 3A and B). The proportions of dark gray and black dots were parametrically varied, and data from the mixed stimuli were compared to those from the uniform stimuli using the normalized unitary perception index defined above. According to the Gestalt principle of grouping by common brightness, there should be more unitary perception of the uniform luminance stimuli than the mixed luminance stimuli. The data support this hypothesis (Fig. 3C, solid circles), and the presence of as little as 5% of dots of a secondary brightness (that is, 95% black/5% dark gray or 95% dark gray/5% black) was sufficient to substantially reduce unitary perception of these stimuli relative to arrays of uniform luminance.

In principle, this grouping effect could be due to an increased frequency of unitary percepts and/or an increase in the average duration of unitary percepts. These values were computed and normalized for each subject using the unitary perception contrast index described above. It is clear that the greater unitary perception associated with uniform luminance arrays was due entirely to an increase in the number of unitary percepts elicited by these stimuli (Fig. 3D, solid circles). There was no change in the average duration of unitary percepts (Fig. 3E, solid circles). Thus, grouping based on common luminance increased unitary perception by facilitating the initiation of a unitary percept. Once this unitary percept was formed, its lifetime was entirely independent of the luminance composition of the stimulus. Evidently, a process independent from grouping was responsible for the termination of the unitary percept.

The effects of grouping based on common luminance were only observed for unitary perception of the test arrays (Fig. 3C and D, solid circles). Changes in the luminance composition of the test arrays had no effect on unitary perception of the contralateral reference arrays (Fig. 3C–E, open circles). This absence of change in perception of the contralateral stimulus distinguishes these results from previous studies in which alterations of low level stimulus features such as luminance (Fox & Rasche, 1969) or contrast (Levelt, 1968) changed predominance in binocular rivalry primarily by affecting perception of the unmanipulated contralateral stimulus. These different patterns of results suggest that grouping effects and stimulus strength effects may have distinct mechanisms (see Section 4.8).

3.3. Grouping based on common color

To test the role of color grouping mechanisms in perceptual selection in binocular rivalry, the amounts of unitary perception of mixed red/green dot arrays were compared to those of uniform red or uniform green arrays. All colored dots were darker than the gray background. For each trial, one of the colored arrays
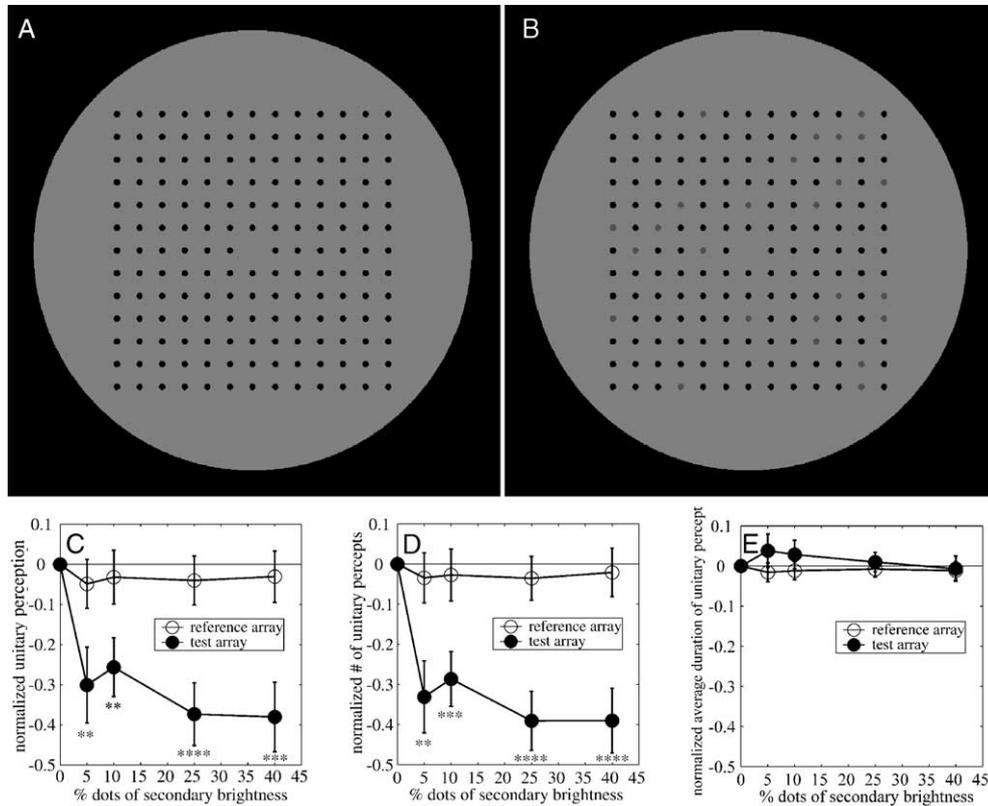
Fig. 3. Grouping based on common brightness. A reference array of gray dots lighter than the background was present for all trials. A test array of dots darker than the background was presented to the other eye, and the individual dots could be either dark gray or black. (A) Test array with dots of uniform brightness. (B) Test array with dots of mixed brightness. (C) Mixed brightness arrays rivaling with a fixed reference array always produced less unitary perception than uniform brightness arrays rivaling with the same reference array, even for arrays in which 95% of the dots had the same luminance. Unitary perception of the test array (solid circles) and reference array (open circles) was measured separately for each proportion of mixed dots (95%/5%, 90%/10%, 75%/25%, and 60%/40%), and the amount of unitary perception was compared to unitary perception in the uniform condition for each experiment in the form of a contrast index. Error bars indicate standard errors of the mean of the contrast index values. Two-tailed t-tests were performed to test whether the means were significantly different from zero. The normalized unitary perception value of -0.38 for test arrays for 40% dots of secondary brightness corresponds to a decrease of 55% relative to uniform luminance arrays. These results indicate that grouping based on common brightness increased unitary perception of the test array and strengthened the representation of the array as a textured surface. There were no effects of grouping based on common brightness on perception of the contralateral reference array. (D) The number of unitary percepts of the test stimulus was lower for mixed brightness arrays than for uniform brightness arrays (solid circles), but the number of unitary percepts for the reference stimulus was independent of the composition of the test array (open circles). (E) There was no difference between mixed and uniform brightness arrays in the average duration of unitary percepts for either test (solid circles) or reference arrays (open circles). $n = 14$ experiments from 7 subjects; $^{**}p < 0.01$; $^{***}p < 0.001$; $^{****}p < 0.0001$.

was presented to one eye, and a reference array consisting of gray dots lighter than the background was presented to the other eye. Because the previous experiment established that grouping based on common luminance had significant effects on unitary perception, the luminances of the red and green dots were equalized using a modification of the heterochromatic flicker paradigm (see Section 2.2).

Mixed red/green arrays generated less unitary perception of the test arrays than uniform arrays of red or green dots (Fig. 4A, solid circles), although the effect only reached statistical significance for the most asymmetric combinations of colors (95%/5% or 90%/10% mixtures). This result was reinforced by the subjects' verbal reports, in which they described a perception of red/green segmentation for the more asymmetric mix-

tures. For example, for the 95% green/5% red stimulus, subjects often reported seeing a combination of red and light gray dots but no green dots. This suggests that the green and red dots may have been grouped separately (perhaps due to figure/ground segmentation mechanisms) and may have independently rivaled with the light gray dots from the other eye, thus reducing unitary perception of the colored array. For the stimuli with more equal numbers of dots, the perception of segregation of red and green dots was less common, and the red and green dots were seen to rival together more often, resulting in increased levels of unitary perception. It may be that figure/ground segmentation is less likely for dot arrays consisting of red and green dots in equal numbers and more likely when a small number of dots of one color can be perceived as a figure surrounded by a
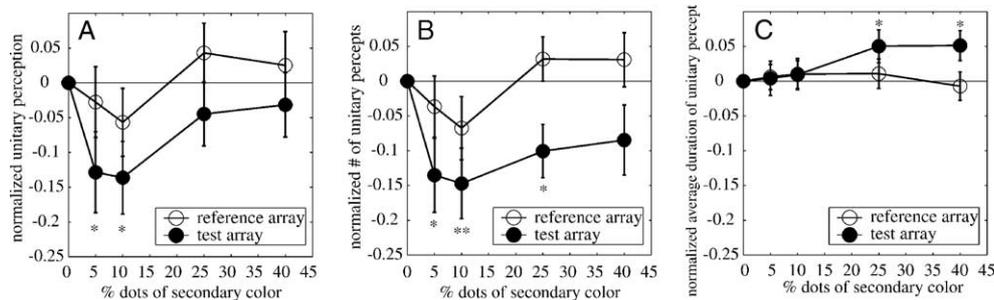
Fig. 4. Grouping based on common color. A test array of either all green dots, all red dots, or a mixture of the two colors was presented to one eye, and a reference array of light gray dots was presented to the other eye. (A) For the test stimuli, arrays of mixed color resulted in less unitary perception than arrays of uniform color, and this difference reached statistical significance for 95%/5% and 90%/10% mixtures (solid circles). Error bars indicate standard errors of the mean. The normalized unitary perception value of −0.14 for test arrays with 10% dots of secondary color corresponds to a decrease of 24% relative to uniform color arrays. Thus, grouping based on common color increased unitary perception in binocular rivalry compared to mixed arrays in which only a small fraction of the dots were of a secondary color. Unitary perception of the reference arrays was unaffected by changes in the color composition of the test array (open circles). (B) Mixed color arrays produced fewer unitary percepts than uniform color arrays for the test arrays (solid circles), but mixed and uniform color arrays resulted in the same number of unitary percepts of the reference arrays (open circles). (C) For test arrays, the average duration of unitary percepts was greater for 60%/40% and 75%/25% mixtures than for uniform color arrays (solid circles). Varying the red/green proportion in the test arrays had no effect on average duration of unitary percepts of the reference arrays (open circles). $n = 14$ experiments from 7 subjects; $^*p < 0.05$; $^{**}p < 0.01$.

background of dots of the other color. In any case, uniformly colored arrays produced more unitary perception than arrays of mixed colors, consistent with grouping based on common color. This effect, although significant for dot arrays with asymmetric proportions of the two colors, was substantially less than the effects due to grouping by common brightness (see Section 4.2).

The effect of grouping by common color was somewhat stronger as measured by the number of unitary percepts, especially for test stimuli with more equal numbers of red and green dots (75%/25% or 60%/40%) (Fig. 4B, solid circles). Surprisingly, the average duration of unitary percepts was greater for these stimuli than for the uniform red or green arrays (Fig. 4C, solid circles). In other words, the 75%/25% mixtures produced unitary percepts less often than the uniform color stimuli, but the durations of these unitary percepts were greater than those produced by the uniform arrays. While the former result is predicted by grouping based on common color, the latter is not. As in the luminance experiments, there was no evidence for color grouping effects on unitary perception, the number of unitary percepts, or the average duration of unitary percepts for the contralateral reference array (Fig. 4A–C, open circles).

3.4. Motion coherence and unitary perception

Objects sharing common directions and speeds of motion are typically combined by the visual system. This is the principle of grouping by common fate. We tested the role of grouping based on coherent motion in arrays of moving dots (test arrays) that were rivaling against stationary arrays of dots with the opposite contrast relative to background (reference arrays). The motion of each dot consisted of a displacement of 0.045 deg at a

speed of 0.8 deg/s from the starting point in the array. The dots then immediately returned to their starting positions along the same path. Upon reaching the starting position, they were again displaced in a different randomly chosen direction and again returned to the starting location. The displacement and return each were 55.6 ms in duration, and this procedure was repeated for the entire 60 s trial. For 100% coherent motion, all of the dots in the array moved synchronously and with the same motion trajectories (Fig. 5A; Movie 1A). For completely incoherent motion (0% coherence), the phases and angles of the individual dot motions were independent and random with respect to each other (Fig. 5B; Movie 1B). The percentage of coherently moving dots was parametrically varied, and unitary perception of the moving and stationary arrays were measured across all conditions. Examples of all the motion stimuli used in this paper can be viewed at socrates.berkeley.edu/~masilver/dotsurf

If coherent motion facilitated grouping of the dots, the amount of unitary perception of the test arrays should have increased as a function of motion coherence. However, the opposite result was obtained: test arrays of incoherently moving dots produced more unitary perception than coherently moving dots, and unitary perception was a monotonic function of the percentage of motion *incoherence* (Fig. 5C, solid circles). This result was due to both an effect of motion incoherence on the number of unitary percepts (Fig. 5D, solid circles) and on the average duration of unitary percepts (Fig. 5E, solid circles).

The amount of incoherent motion in the test arrays had essentially no effect on the amount of unitary perception, the number of unitary percepts, or the average duration of unitary percepts for the static reference ar-
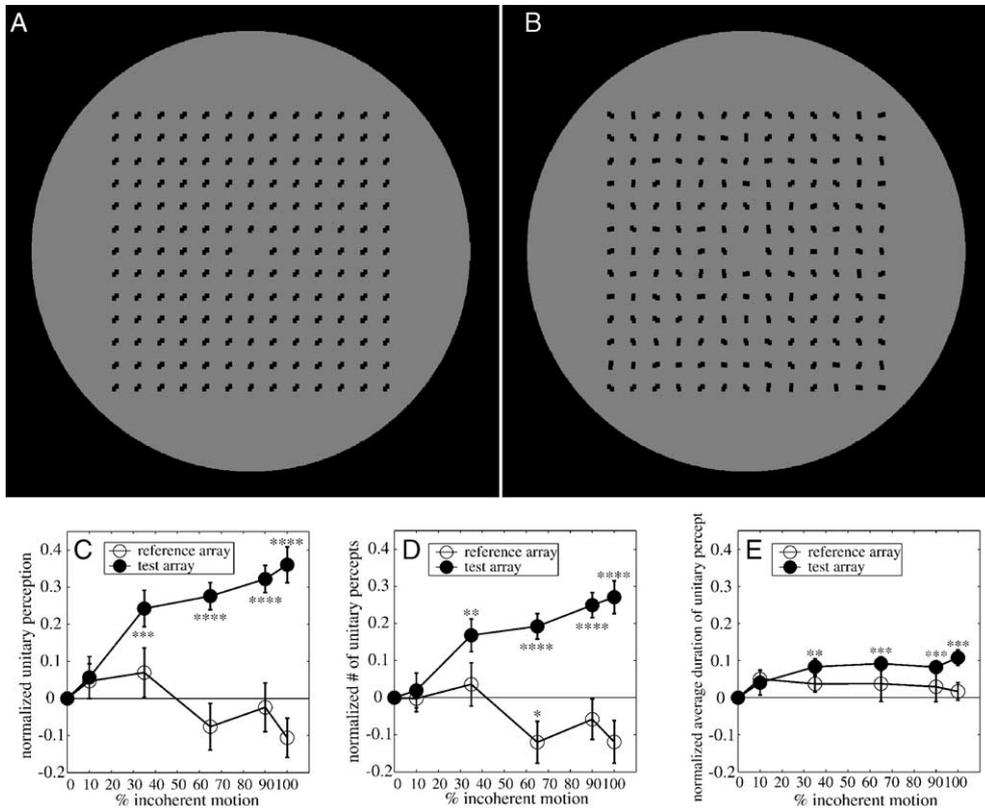
Fig. 5. Test arrays with incoherent motion generated more unitary perception than arrays with coherent motion. Arrays of dots with varying amounts of motion coherence (test arrays) rivaled with reference arrays consisting of stationary dots, and the amount of unitary perception of both test and reference arrays was measured. (A) Completely coherent motion (0% motion incoherence). (B) Completely incoherent motion. The stimuli shown here are scaled versions of the actual arrays used in the experiments, and one full displacement of 0.045 deg is shown for each dot. The examples shown here correspond to arrays that subtended 8×8 deg of visual angle. (C) Although grouping based on common motion would have resulted in less unitary perception for incoherent than coherent motion in the test arrays, the opposite result was obtained. Increases in motion incoherence produced a monotonic increase in unitary perception of test arrays (solid circles). The normalized unitary perception value of 0.36 for test arrays with 100% incoherent motion corresponds to an increase of 113% relative to test arrays with completely coherent motion. There was no effect of variation of test array motion coherence on unitary perception of the static reference arrays (open circles). (D) For the test arrays (solid circles), but not the reference arrays (open circles), the number of unitary percepts increased as a function of motion incoherence in the test arrays. (E) The average duration of unitary percepts of the test arrays increased as a function of test array motion incoherence (solid circles), but this measure for the reference arrays was unaffected by variation in test array motion coherence (open circles). $n = 17$ experiments from 9 subjects; $^*p < 0.05$; $^{**}p < 0.01$; $^{***}p < 0.001$; $^{****}p < 0.0001$.

rays (Fig. 5C–E, open circles). The single exception was that the number of unitary percepts for a reference array rivaling with a moving test array containing 65% incoherent motion was lower than the number of unitary percepts of the same reference array rivaling with a moving test array with completely coherent motion ($p = 0.048$, Fig. 5D, open circles). This is the only example in all of the luminance, color, and motion coherence experiments in which variations in the composition of the test array resulted in changes in unitary perception of the contralateral reference array. Given the number of comparisons made in analysis of the unitary perception data for the reference arrays (total of 39), we do not consider this single positive result with $p = 0.048$ to have much importance. For luminance and color, the statistical power of these tests were approximately equal for the test and reference arrays, because the contrasts of the arrays were set so that they would

have approximately equal strengths in rivalry (see Section 2.2). For the motion coherence experiments, there is a caveat concerning these negative results. Moving stimuli have a significant advantage over stationary stimuli in binocular rivalry, regardless of whether the motion is coherent or incoherent (Blake, Yu, Lokey, & Norman, 1998), and the amount of unitary perception of the static reference arrays in these experiments was much less than the amount of unitary perception of the moving test arrays. Thus, the finding that there was no effect of test array motion coherence on unitary perception of the contralateral static reference array should be interpreted with caution.

3.5. Segmentation and collinearity in binocular rivalry

The finding that unitary perception of test arrays with incoherent motion was greater than unitary perception

of coherently moving arrays was initially surprising, given the principle of grouping by common fate. However, dot arrays with high amounts of motion coherence also contain moving rows and columns that could be perceived as moving contours. Collinearities, in the form of coherently moving rows and columns of dots, may have acted as segmentation cues to partition the moving array, thereby disrupting perception of the array as a uniform surface and decreasing unitary perception. The possible significance of collinearities in the perception of these arrays was suggested even in subjects' verbal reports from pilot experiments using the stimuli shown in Fig. 1A. Subjects reported that the boundaries of the regions of exclusive dominance seen in piecemeal rivalry (Fig. 1C) were often oriented along the vertical and horizontal axes. In addition, these perceptual boundaries were not static but rather swept across the dot arrays as traveling waves. The direction of movement of the perceptual boundaries was typically along the vertical or horizontal axes. While we cannot exclude the possibility that the cardinal axes have some special role in the perception of these stimuli, it seems more likely that the orientation and direction of motion of the perceptual boundaries are due to the horizontal and vertical collinearities present in the arrays. The phenomenon of moving boundaries of dominance in piecemeal rivalry is well known and has been modeled as a wave of activity traveling across visual cortex (Wilson, Blake, & Lee, 2001). In these experiments, the traveling waves also followed the shape of the stimulus and in fact propagated in a circular trajectory around the annular stimulus.

We performed several experiments to test whether the presence of collinearity reduced unitary perception. First, we disrupted collinearities in rivalrous arrays of static dots by introducing positional jitter. Beginning with the stimuli in Fig. 1A, stimuli were generated in which each dot was displaced both horizontally and vertically. These distances were randomly and independently selected from a range of values, and the range varied from ±0.045 to ±0.13 deg, depending on the experiment. This procedure was carried out for both eyes' stimuli, although the exact displacements were completely random for each dot. Therefore, there was no systematic relationship in the directions or magnitude of displacement in the two eyes. Unitary perception of each eye's stimulus was combined and compared to arrays without jitter. The resulting contrast index value was 0.071 ± 0.042, indicating that the presence of positional jitter increased unitary perception. However, this value, although statistically significant ($p < 0.05$), was quite small compared to most of the other effects described in this paper, corresponding to approximately a 15% increase in unitary perception. Thus, although the results of this experiment support the notion that collinearities disrupt unitary perception, the effect size was

small. This suggests that there may be a fundamental difference between moving and stationary collinearities in the grouping and segmentation processes underlying perception of these stimuli.

3.6. Moving collinearities and unitary perception

To test the role of motion collinearities more directly, we generated stimuli that contained stimuli with coherent motion but without motion collinearities. This was accomplished by using concentric dot motion (Fig. 6B; Movie 2). In this case, each dot oscillated along fixed trajectories emanating from the fixation point. The speed and displacement of the motion were identical to the motion shown in Fig. 5A and B and in Movie 1, which will be referred to as "dynamic jitter". For coherent concentric motion (Movie 2A), the dots moved synchronously away and towards the fixation point, creating the impression that the array was alternately expanding and contracting. For incoherent concentric motion (Movie 2B), the local motion of each dot was exactly the same as in the coherent case, but the angles and phases of the individual dot oscillations were randomized for the arrays with incoherent motion.

The key difference between coherent dynamic jitter and coherent concentric motion is that coherent dynamic jitter has motion collinearities in the rows and columns of the arrays, while concentric coherent motion does not (compare Fig. 6A and B; Movies 1A and 2A). Therefore, if motion collinearities were responsible for segmentation of the moving array and the resulting loss of unitary perception, the effect of introducing incoherent motion should have been much less for concentric motion than for dynamic jitter. The data support this hypothesis (Fig. 6C). Although incoherent motion increased unitary perception of dot arrays consisting of dynamic jitter, this effect was greatly reduced or abolished for concentrically moving stimuli. We propose that incoherent motion disrupted moving collinearities for dynamic jitter, but because there were no collinearities in the arrays with coherent concentric motion, the effects of adding incoherent motion were minimal.

For the dynamic jitter stimuli, the incoherently moving dots had both randomized phases and angles of motion. The fact that more unitary perception occurred for incoherent motion than for coherent motion could have been due to the fact that the motion trajectories of the individual dots generated moving collinearities. Alternatively, since the displacements of the coherently moving dots were synchronized, the greater unitary perception for incoherent motion compared to coherent motion could have been due to simultaneous changes in the direction of movement of the individual dots for coherent motion. Subjects can segregate figure from ground in arrays of rotating elements for temporal differences between figure and ground rotation of
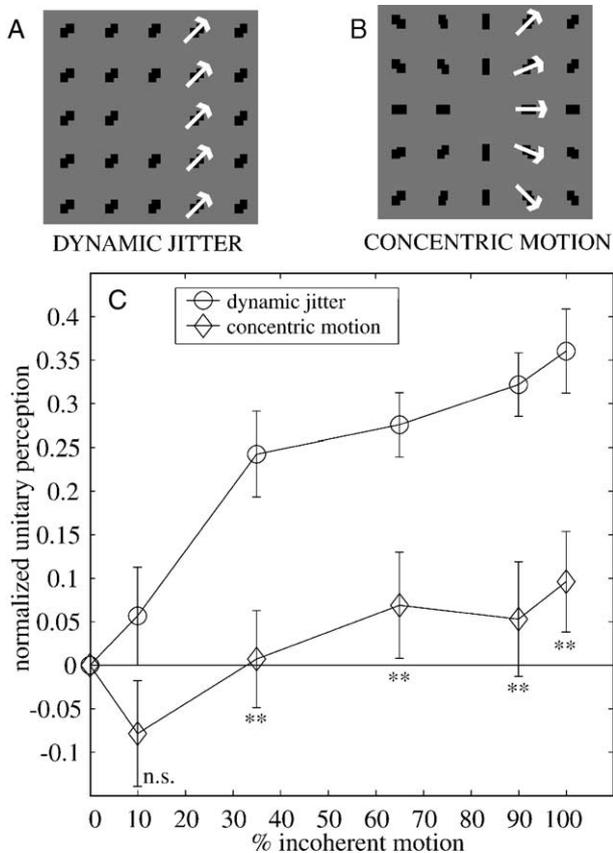
Fig. 6. Effects of motion coherence were not observed for concentrically moving stimuli without motion collinearities. (A) Completely coherent dynamic jitter. This stimulus contains motion collinearities in the rows and columns of the array (*white arrows*). (B) Completely coherent concentric motion. Although the phases of the motion of individual dots were synchronized, the motion trajectories were along radii emanating from the fixation point (*white arrows*). Therefore, collinearity of the rows and columns was not preserved. (C) *Circles* indicate the dynamic jitter data from Fig. 5C, replotted here for comparison with the other stimuli. *Diamonds* indicate the amount of unitary perception for concentrically moving stimuli as a function of motion incoherence. The arrays with preserved motion collinearity (dynamic jitter) had a significantly greater effect of motion coherence on unitary perception than the stimuli without moving collinearity (concentric motion). This is consistent with the hypothesis that moving collinearities reduce unitary perception by activating segmentation mechanisms. Two-tailed *t*-tests were performed to determine whether the normalized unitary perception contrast indices differed between dynamic jitter and concentric motion. $n = 18$ experiments from 9 subjects; ** $p < 0.01$; n.s., not significant.

approximately 10 ms (Kandil & Fahle, 2001), and detection of contours consisting of drifting Gabor patches is enhanced if reversals of direction of grating motion of the patches are synchronized (Lee & Blake, 2001).

To determine whether the synchronized motion displacements in the coherently moving arrays impaired unitary perception, a set of dynamic jitter stimuli was created in which the phases of motion were synchronous for all levels of motion coherence. These will be referred to as "uniform phase" stimuli. Coherence was para-

metrically varied, but only the angles of motion were randomized for the incoherently moving dots. For uniform phase stimuli with coherent motion (Movie 3A), the motion was indistinguishable from the dynamic jitter stimuli shown in Fig. 5A and Movie 1A, since coherent motion requires that the phases be uniform. For incoherent motion (Movie 3B), uniform phase requires that all of the dots are displaced at the same time and return to the starting point at the same time (of course, the direction of the displacement was randomized for each dot).

Synchronization of the dot motion had little or no effect on relative unitary perception compared to dynamic jitter stimuli without synchronization (compare circles and triangles in Fig. 7). Thus, the increase in unitary perception as a function of motion incoherence was not dependent on differences in the phases of motion of incoherently moving dots. For dynamic jitter with uniform phase, the most obvious difference between coherent and incoherent motion is the presence of motion collinearities in the coherently moving stimuli.

As a final test of the role of motion collinearities in segmentation of rivalrous dot arrays, we compared three
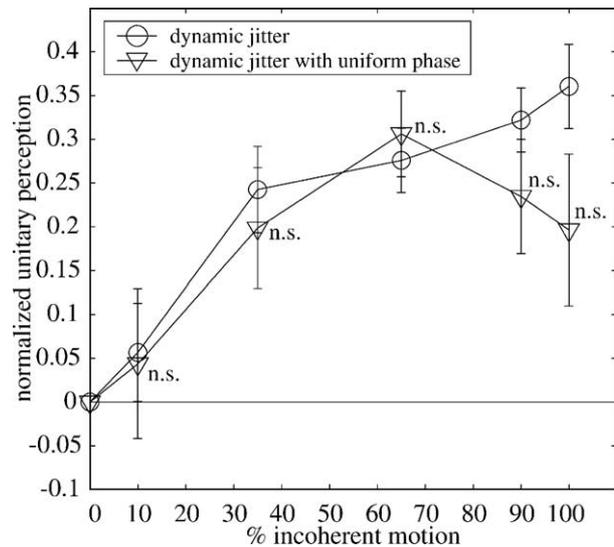

Fig. 7. The effects of motion coherence are not due to synchronization of either motion displacements or changes in direction of motion. *Circles* indicate the dynamic jitter data from Fig. 5C, replotted here for comparison with the other stimuli. *Triangles* indicate dynamic jitter with uniform phase. For the uniform phase stimuli, the phases of the motion were synchronized for each level of motion coherence; the only difference between 0% and 100% motion incoherence was in the angles of movement of the individual dots. These arrays produced an increase in unitary perception as a function of motion incoherence that was indistinguishable from the dynamic jitter stimuli. Since all of the dot displacements were synchronous, the result is likely to be due to decreased motion collinearity in arrays with incoherent motion. Two-tailed *t*-tests were performed to determine whether the unitary perception was different between dynamic jitter and dynamic jitter with uniform phase. $n = 14$ experiments from 7 subjects; n.s., not significant.

different types of stimuli, all of which oscillated along motion trajectories either 45 or 135 deg from vertical. Motion in the arrays was completely coherent (Movie 4A), coherent only at the level of individual rows or columns (Movie 4B), or completely incoherent (Movie 4C). Because the angle of motion was identical for all the dots in the arrays, the difference between coherent and incoherent motion was entirely in the phases of
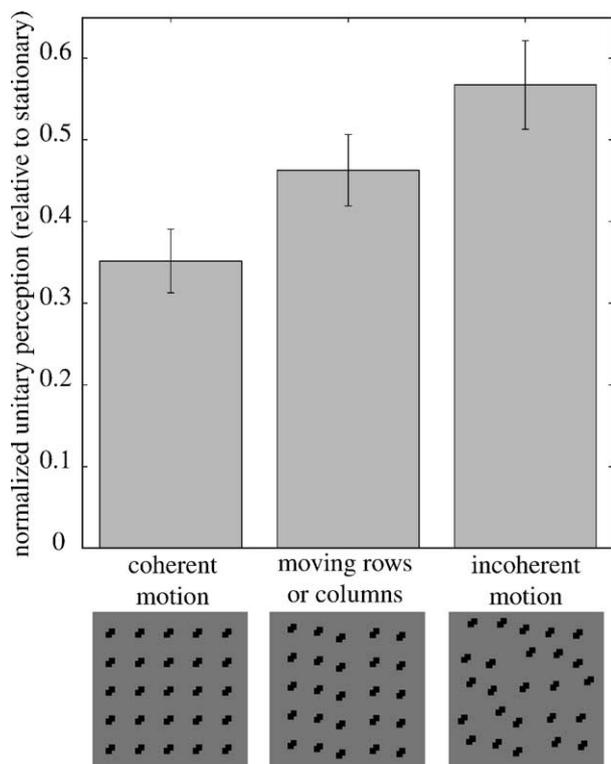

Fig. 8. Unitary perception is inversely related to the amount of motion collinearity in the stimulus. Stimuli that had identical angles of movement but differed in the relative phases of movement were employed. All dots moved along a diagonal axis. In the coherent case, all of the dots moved along this axis in phase. In the "rows or columns" case, the dots moved synchronously within either rows or columns, but the phases of motion of these rows or columns were independent of one another. The phases of motion of individual dots in the incoherent motion stimuli were fully randomized. Unitary perception data were plotted as contrast indices relative to values of unitary perception obtained from static dot arrays. Schematic representations of the stimuli are shown below the graph. They represent only a portion of the entire array and are not to scale. The coherent motion stimulus had the most motion collinearity (both rows and columns are collinear) and the lowest amount of unitary perception. The "rows or columns" stimuli have motion collinearity along only one dimension and intermediate levels of unitary perception. The incoherently moving stimuli have no motion collinearity and the highest amount of unitary perception. Direct comparisons between "rows or columns" and coherent motion in the form of a contrast index (as opposed to the contrast indices shown in the bar graph which were calculated relative to arrays of stationary dots) resulted in a value of 0.17 ± 0.06, and this was significant at $p < 0.01$. A direct comparison between incoherent motion and "rows and columns" produced a contrast index of 0.15 ± 0.04, and this was significant at $p < 1 \times 10^{-3}$. $n = 17$ experiments from 7 subjects.

motion. In the coherent motion case, all the phases were identical. For incoherent motion, the phases of the individual dot motions were completely randomized. For the third case, called "rows or columns", the phases of motion in single rows or columns were identical, but there was no temporal relationship among the rows or columns. A given trial with "rows and columns" stimuli consisted either of coherent motion of rows or of columns. Arrays with completely coherent motion contained both horizontal and vertical motion collinearities, since the motion of all of the dots in the array were synchronized. As in all the motion experiments, the local motions of the dots were indistinguishable across conditions. However, the three classes of stimuli differed in the amount of motion collinearity they contained. The incoherent motion stimuli had no motion collinearities, the "rows or columns" stimuli had motion collinearities in one dimension (horizontal or vertical), and the arrays consisting of completely coherent motion had the most motion collinearity (both rows and columns contained collinearities). If moving collinearities act as segmentation cues to reduce unitary perception, the amount of unitary perception in the three types of arrays should be (incoherent) > (rows or columns) > coherent). These results were obtained (Fig. 8). The amount of unitary perception was inversely proportional to the amount of motion collinearity in the stimuli.

4. Discussion

The results of this paper demonstrate that grouping on the bases of common luminance and common color increases unitary perception in binocular rivalry. Arrays of dots of uniform luminance or color produced significantly more unitary perception than arrays containing dots of mixed luminance or color. Previous work has also demonstrated grouping in binocular rivalry on the basis of good continuation (Alais & Blake, 1999). Pairs of gratings that were spatially separated but collinear tended to rival together as though they were grouped by the visual system into a single oriented object viewed through two occluders. In addition, correlated temporal modulations of contrast in the gratings also resulted in grouping (Alais & Blake, 1999). Interocular grouping in binocular rivalry has also been reported for a variety of stimuli (Diaz-Caneja, 1928; Kovács et al., 1996; Leopold, 1997; Suzuki & Grabowecky, 2002). Finally, rapid (3 Hz) interocular switching of rivalrous gratings can result in periods of perception of only one grating that span several stimulus switches, indicating interocular grouping across time (Logothetis, Leopold, & Sheinberg, 1996).

These results and the findings from the present study illustrate how binocular rivalry can be used as a tool for revealing grouping and segmentation processes in the

visual system. For many visual stimuli, grouping and image segmentation occur so effortlessly and automatically that it is difficult to measure the underlying processes psychophysically or to report on their phenomenology. One approach to this problem has been to use stimuli that are difficult to detect or discriminate. For example, if stimuli have very low contrast, are presented for brief durations, or are masked by other stimuli, grouping and segmentation processes can be more easily studied. Binocular rivalry provides a means of quantitatively investigating grouping and segmentation without requiring the use of stimuli at the threshold of detection.

4.1. State transitions in binocular rivalry

We have shown that a period of unitary perception of one stimulus tends to be immediately followed by unitary perception of the other stimulus. This is true even though the mixed percept occurs for the majority of the viewing time. Therefore, it appears that the visual system can enter a mode in which the arrays compete at the level of surfaces. This mode is characterized by alternation between unitary percepts. In the other mode, competition occurs between portions of the stimulus, and consequently piecemeal rivalry is observed. These results are reminiscent of the perceptual trapping described by Suzuki and Grabowecky (2002). They used multistable binocular rivalry and computed the probabilities of transitions from one percept to another. These probabilities deviated from those expected if the various percepts were independent. This result is consistent with the notion that the visual system can support multiple levels of competition for a given set of stimuli (Bonneh et al., 2001). It should be noted that this aspect of multistable perception has been obscured in binocular rivalry experiments in which subjects report which of two rivalrous stimuli is more dominant (the standard two alternative forced choice paradigm).

4.2. Luminance- versus color-based grouping

Although the experiments presented in this paper provide evidence for grouping based on both luminance and on color, the effects of luminance-based grouping were much greater than those obtained for color. A previous study by McIlhagga and Mullen (1996) also indicated that grouping by luminance is more powerful than grouping by color. They found that the threshold for detection of contours consisting of Gabor patches with luminance contrast was less than that for contours made of equiluminant Gabor patches with color contrast. This was true even when the orientation discrimination thresholds of the individual elements were equalized, indicating that the visual system combines luminance-defined elements more easily than color-defined elements (McIlhagga & Mullen, 1996). Taken together, these results suggest that luminance is a stronger cue for grouping than color.

4.3. Collinearity detectors in the visual system

We have found that unitary perception of rivalrous dot arrays is influenced by segmentation based on collinearities in the stimuli. For the dot arrays used in these experiments, the most common percept was piecemeal rivalry, in which complementary regions of each array dominated over corresponding regions in the other stimulus. The boundaries of these regions and the motion of the boundaries obeyed the vertical and horizontal collinearities present in the arrays. Additionally, stationary arrays with positional jitter that disrupted collinearity produced more unitary perception than collinear arrays.

In natural vision, continuous contours are a strong cue for segregation of objects. However, the visual system also appears to be specialized for detecting collinearities with gaps between contour fragments. This may allow for the integration of contours corresponding to straight object boundaries interrupted by occluders. Straight contours made of spatially separated Gabor patches are easier to detect than curved contours (Hess, Beaudot, & Mullen, 2001), and they are also detected more rapidly (Beaudot & Mullen, 2001). In addition, detectability of circular contours composed of Gabor patches is facilitated if the orientations of the elements are collinear (smooth contour) compared to contours containing elements that are rotated relative to the contour (jagged contour), and this was true both for detection at threshold contrasts as well as detection in noise (Bonneh & Sagi, 1998). Similarly, smooth contours are more dominant than jagged contours in binocular rivalry (Bonneh & Sagi, 1999). Detection of a line segment is facilitated if the segment is flanked along its orientation axis by collinear line segments (Kapadia, Ito, Gilbert, & Westheimer, 1995), and this facilitation disappears if the flanking line segments are displaced as little as 10 arcmin of visual angle from the collinear configuration. In addition, facilitation is greater if there is a 30 arcmin gap between the target and the flanking stimuli than if flanking stimuli are continuous with the target (Kapadia et al., 1995). Finally, lines containing periodic gaps are suppressed less frequently than continuous lines in binocular rivalry (Burke, Alais, & Wenderoth, 1999).

Of course, Gabor patches and oriented line segments will activate orientation-selective V1 neurons very differently from the unoriented dot elements used in this study. However, there is considerable evidence for collinearity detectors even for spaced elements with no local orientation. For dot size:dot spacing ratios of less than about 1:5, lines of dots generate the same depth

and subjective brightness illusions as continuous contours (Zucker & Davis, 1988). This ratio appears to be critical, as more sparsely spaced dots do not produce the illusions (the dot size:dot spacing ratio for the arrays used in the present study is 1:2.6). Additionally, detection of a target consisting of collinear dots embedded in a background of dots is impaired when positional jitter is introduced into the target (Uttal, 1975).

4.4. Collinearity and motion

Although collinearities reduced unitary perception even for static rivalrous stimuli, their effects were much more pronounced in stimuli containing moving dots. Previous work on the detection of moving contours containing gaps supports the importance of motion collinearities. Detection of a target group of four dots on a background of randomly moving dots was significantly enhanced if the four dots were collinear and if the motion trajectories were parallel (Uttal, Spillmann, Stürzel, & Sekuler, 2000). Similarly, moving contours consisting of unoriented patches of pixellated noise moving in the same direction along the axis of the contour are more easily detected if the contour is straight or has low curvature (Ledgeway & Hess, 2002). Although these experiments were concerned with detection of moving contours and did not require segmentation of a larger stimulus into smaller regions on the basis of moving collinearities, they do indicate that the motion system has a preference for moving collinearities compared to non-collinear stimuli.

Previous results indicate that grouping based on common motion may not occur at all in binocular rivalry (Blake et al., 1998). When rivaling against a field of randomly placed static dots, coherently and incoherently moving dots generated the same amount of unitary perception. This suggests that grouping on the basis of coherent motion had no effect on unitary perception in binocular rivalry. The equivalence of coherent and incoherent motion is in contradiction to the results of the present study, in which incoherent motion resulted in significantly more unitary perception than coherent motion. We propose that the difference between incoherent and coherent motion in our study was due to the presence of motion collinearities in the coherently moving stimuli. In the Blake et al. (1998) study, coherently moving dots shared the same speed and direction of motion, but their locations were randomized. Therefore, there were no motion collinearities in any of their stimuli, and consequently there were no differences between the amount of unitary perception of incoherent and coherent motion. In our experiments with arrays of concentrically moving dots that contained no motion collinearities (Movie 2A), we also observed that unitary perception was largely independent of the amount of motion coherence (diamonds in Fig. 6C).

4.5. Possible contributions of isodirectional surround inhibition of motion detectors

The effects of motion coherence on unitary perception in the present study have been interpreted in terms of motion collinearities acting as segmentation cues. However, dot arrays with high levels of motion coherence may generate lateral inhibition between motion detectors tuned to the same direction of motion. Neurons in cortical area MT have center-surround receptive fields and respond best to opposing directions of motion in the center and surround (Allman, Miezin, & McGuinness, 1985). The responses of these neurons to a stimulus in the classical receptive field that is moving in the neuron's preferred direction are diminished by simultaneous presentation of a surround stimulus moving in the same direction. In addition, the perceived contrast of a drifting circular grating is decreased if it is surrounded by an annular grating with the same speed and direction of motion (Takeuchi & De Valois, 2000). If isodirectional surround inhibition occurred for uniform motion stimuli in the present study, it could have weakened the representation of these stimuli, thereby reducing their levels of unitary perception relative to stimuli with incoherent motion.

The relative contributions of segmentation based on collinearity and isodirectional surround inhibition are difficult to separate. For square lattice arrays like the ones used in this paper, any manipulation that changes the proportion of dots in the surround that share the same motion trajectory as the central dot will also have similar effects on the amount of collinearity in the stimulus. However, the subjective verbal reports of the participants in this study favor an explanation based on collinearity detection. Subjects frequently reported perceptual boundaries between regions of exclusive dominance for both static and moving dot arrays. These boundaries typically were oriented along the vertical and horizontal axes and moved across the arrays in a direction perpendicular to the boundary axis. Given that the collinearities in the dot arrays were also along the vertical and horizontal axes, these results are consistent with an important role for segmentation based on collinearity detection in the perception of these stimuli. In contrast, isodirectional surround inhibition would not be expected to be restricted to the cardinal axes. However, further experiments will be required to determine the possible contribution of isodirectional surround inhibition to the effects of motion coherence on unitary perception in binocular rivalry.

4.6. Potential confounds due to eye movements

For dynamic jitter stimuli, coherent and incoherent motion differ in the amount of motion collinearity. Another possible difference is that coherent wide-field

motion could cause eye movements that would not occur for stimuli with incoherent motion. If this were the case, and if the eye movements disrupted unitary perception, this could account for the results reported in this paper. In principle, dichoptic wide-field motion could cause two types of eye movements. The first is conjugate ocular following eye movements. These are thought to compensate for wide-field movement in the frontoparallel plane relative to the observer. If ocular following eye movements were elicited by coherent motion in the rivalry experiments, they should have occurred for dynamic jitter but not for concentric motion. The second type of eye movement that could have been elicited by the coherently moving dot arrays is vergence corrective eye movements. Such movements have been described for binocularly fused random dot patterns in which binocular disparity is altered by a sudden displacement of one of the patterns (Rashbass & Westheimer, 1961). Vergence eye movements are thought to allow the visual system to maintain binocular alignment to compensate for changes in distance between the observer and objects in the fixation plane. They occur even if the patterns are of opposite contrast in the two eyes and rival with one another (Masson, Busettini, & Miles, 1997), indicating that stereoscopic depth perception is not required.

There are a number of reasons to believe that eye movements did not significantly contribute to our results. The finding that there was more unitary perception for incoherent motion (Movie 4C; Fig. 8, right) than for coherently moving rows or columns (Movie 4B; Fig. 8, center) argues against the possibility of a confound due to ocular following eye movements. There was no global motion signal for either coherently moving rows or columns or for incoherent motion, and neither stimulus should have produced either vergence or ocular following eye movements. Nevertheless, the amount of unitary perception was greater for incoherent motion than it was for coherently moving rows or columns. The most obvious difference between these two stimuli is that one contains motion collinearities and the other does not.

Additionally, we find it unlikely that significant eye movements occurred in response to the motion stimuli in our experiments. The shortest reported latencies are 70–75 ms for ocular following eye movements (Gellman, Carl, & Miles, 1990) and 80 ms for vergence eye movements (Masson et al., 1997). For the dynamic jitter experiments described in the present study, the entire 0.045 deg displacement from the starting position had a duration of 56 ms, and it took another 56 ms for the dots to return to their starting positions. Therefore, it seems very improbable that systems with minimum latencies of 70 ms could generate substantial eye movements in response to motion that is changing direction every 56 ms. In addition, subjects were in-

structed to maintain fixation for the duration of the trial, and vergence cues were employed to minimize eye movements (see Section 2.2).

4.7. Grouping versus segmentation in visual processing

Two very different types of results were obtained in the binocular rivalry experiments described in this paper. For color and luminance, grouping processes were revealed: stimuli of uniform color or luminance produced more unitary perception than stimuli with mixed color or luminance. For motion, however, stimuli with incoherent motion resulted in more unitary perception than stimuli with coherent motion, indicating segmentation rather than grouping on the basis of motion coherence.

Neurophysiological studies have shown that motion boundaries may be encoded relatively early in the visual pathways, while analysis of local motion occurs later. Some of the neurons in cortical area V2 in the macaque monkey have orientation selectivity for boundaries defined exclusively by motion, and the preferred orientation for these boundaries is similar to the preferred orientation for luminance-defined boundaries, indicating that these neurons may signal the presence of a boundary at a specific location and orientation, regardless of the type of boundary (Marcar, Xiao, Raiguel, Maes, & Orban, 1995). Neurons in cortical area MT, on the other hand, respond exclusively to local motion signals and do not have selectivity for the orientation of motion-defined boundaries that is independent of these local signals (Marcar, Raiguel, Xiao, & Orban, 2000). Although MT neurons do not appear to be important for segmentation based on motion, their activity is consistent with a role in grouping based on common motion. The firing rate of MT neurons signals the amount of motion coherence in random dot kinematograms (Britten, Shadlen, Newsome, & Movshon, 1993), and the distance over which individual directionally-selective neurons pool motion signals is approximately three times larger in MT than V1 (Mikami, Newsome, & Wurtz, 1986). Together, these results suggest that coding of motion boundaries may precede more detailed analysis of the motion vectors across the visual field, including grouping on the basis of coherent motion.

Early segmentation based on boundaries followed by slower grouping processes could account for the effects of motion coherence on unitary perception. In the presence of even a small amount of coherent motion, boundary detection would occur and would segment the dot array, thereby reducing unitary perception. Even if grouping based on common motion did take place, it would occur within regions of the stimulus that had already been segmented and would therefore have no effect on the amount of unitary perception.

Other evidence also indicates that boundary detection precedes grouping based on element similarity. Lamme, Rodriguez-Rodriguez, and Spekreijse (1999) presented macaque monkeys with stimuli consisting of a textured figure defined by differences in orientation of texture elements relative to a textured background. When the figure/ground boundary was placed within the receptive field of V1 neurons, response latencies were short. On the other hand, when the receptive fields were located within the figure, there was a delayed enhancement of activity compared to receptive field locations outside the figure (in the background), indicating a process of surface filling that followed encoding of the figure/ground boundaries. A number of theoretical models have also postulated a rapid boundary detection system and a slower system that fills in surfaces (Grossberg & Mingolla, 1985; Roelfsema, Lamme, Spekreijse, & Bosch, 2002).

If segmentation based on boundary detection precedes grouping, why did grouping based on common luminance and common color occur for the rivalrous dot arrays? The physiological and theoretical studies described above pertain to processing of stimuli made of textured elements. It may be that for fundamental low-level stimulus features such as luminance and color, grouping occurs even earlier than boundary detection. Detection of oriented boundaries requires, at the very least, neurons with orientation selectivity, and these neurons are found only in visual cortex. Coding of color and luminance, on the other hand, is present in the retina, and there is evidence that grouping on the basis of common luminance can occur via long-range synchronization of responses within the retina over distances of at least 20 deg of visual angle (Neuenschwander & Singer, 1996). Therefore, at least some grouping of color and luminance may be able to occur before segmentation of the arrays by boundary detectors, allowing stimuli with uniform color and luminance to generate more unitary perception than mixed color and luminance arrays.

4.8. Stimulus strength versus grouping and segmentation in binocular rivalry

All of the stimulus manipulations in this study that affected unitary perception did so by altering the amount of unitary perception and/or the average duration of unitary perception of the manipulated test array, while these measures for the unchanged contralateral reference array were unaffected. This pattern of results is the opposite of that observed by Levelt (1968) following manipulations of contrast. He found that increasing the contrast of one rivalrous stimulus enhanced its predominance by decreasing the mean duration of dominance of the unchanged contralateral stimulus. This pattern has generally been observed for low-level stim-

ulus features such as luminance (Fox & Rasche, 1969), contrast (Blake, 1977), color contrast (Bossink et al., 1993), and motion velocity (Bossink et al., 1993), although small changes in the mean duration of dominance of the changed ipsilateral stimulus have also been reported (Bossink et al., 1993; Mueller & Blake, 1989). The effect described by Levelt has also been observed for rivalrous static dot arrays very similar to the ones used in the present study: increasing the contrast of the dots of one array decreased the average duration of periods of unitary perception of the contralateral array (Leopold, 1997).

In contrast to these results involving variations of low level stimulus features, manipulations involving grouping or spatial relationships among multiple stimuli have typically resulted in changes in the mean duration of dominance of the manipulated stimuli. For orthogonal rivalrous grating patches, the addition of an annulus consisting of random static dots around one of the gratings increased its predominance, and this enhancement was due to an increase in the mean duration of dominance of the grating that had the surrounding annulus (Fukuda & Blake, 1992). Additionally, for stimuli in which a drifting grating patch can be perceived as part of a larger stimulus moving behind occluders or as local independent motion, dominance in rivalry was greater when associated with the global motion percept, and this difference was also due to a change in mean dominance duration for the manipulated stimulus (Sobel & Blake, 2002).

The effects of grouping and segmentation demonstrated in this paper are consistent with this overall pattern in the literature. All of the stimulus manipulations resulted in alterations of mean dominance durations for the manipulated dot array, and no changes were observed in the contralateral reference array. It should also be noted that many of the studies described above used a 2 alternative forced choice paradigm (2AFC), in which observers continuously reported which stimulus was more dominant. This paradigm does not distinguish between unitary percepts and mixed percepts that are dominated more by one stimulus than the other. As a result, dominance of one stimulus is defined to be equivalent to suppression of the other stimulus. In our experiments, subjects reported unitary percepts with a button press and withheld button presses when they experienced mixed percepts. The fact that we observed changes in unitary perception of the manipulated test arrays but no changes in the unmanipulated reference arrays implies that the grouping and segmentation effects we have observed are primarily due to changes in the balance between unitary perception of the test stimuli and mixed percepts.

Additionally, the effects of grouping and segmentation on unitary perception were largely due to changes in the frequency of periods of unitary perception of the

test arrays as opposed to changes in the average duration of unitary percept. Overall, the results suggest that grouping and segmentation primarily affected the probability of a transition from the mixed percept to dominance of the test stimulus and that they had relatively little effect on the average lifetime of the unitary percept once it was established. This conclusion is consistent with the idea that the neural processes underlying dominance and suppression in binocular rivalry may be different (Blake, 2001; Logothetis, 1998). The grouping and segmentation effects we have observed are due to processes that determine whether a stimulus attains dominance or not, and these processes are likely to be separate from those that cause suppression.

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