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Visual Motion Retards Alternations between Conflicting Perceptual Interpretations

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Summary

When the visual system is faced with conflicting or ambiguous stimulus information, visual perception fluctuates over time. We found that perceptual alternations are slowed when inducing stimuli move within the visual field, constantly engaging fresh, unadapted neural tissue. During binocular rivalry, dominance durations were longer when rival figures moved compared to when they were stationary, yielding lower alternation rates. Rate was not reduced, however, when observers tracked the moving targets, keeping the images on approximately the same retinal area. Alternations were reliably triggered when rival targets passed through a local region of the visual field preadapted to one of the rival targets. During viewing of a kinetic globe whose direction of rotation was ambiguous, observers experienced fewer alternations in perceived direction when the globe moved around the visual field or when the globe's axis of rotation changed continuously. Evidently, local neural adaptation is a key ingredient in the instability of perception.

Introduction

The brain is often forced to resolve conflict arising from competing motor tendencies (e.g., approach versus avoid), from uncertainty concerning an ambiguous message's meaning ("the man sat beside the bank"), or from confusion surrounding competing perceptual interpretations (ambiguous figures). In some instances, conflict is resolved at the expense of slow, error-prone behavior, as exemplified by the well-known Stroop interference effect (Stroop, 1935). In the case of visual ambiguity, conflict is typically resolved by successively entertaining alternative perceptual interpretations: rather than selecting and maintaining a single solution, perception vacillates over time between alternatives. One striking example of perceptual multistability occurs when the two eyes view dissimilar patterns, triggering fluctuating periods of dominance and suppression of the two competitors—this is the well-known phenomenon of binocular rivalry (Levelt, 1965; Walker, 1978; Blake, 1989). Another compelling instance of perceptual multistability is experienced when viewing rotating objects whose three-dimensional structure is ambiguous—known as the kinetic depth effect (KDE) (Miles, 1931; Howard, 1961). These two phenomena—binocular rivalry and KDE—provide paradigm conditions for studying perceptual conflict and its neural concomitants (Logothetis, 1998; Leopold and Logothetis, 1999).

Several aspects of multistable perception should be distinguished when considering the underlying neural bases of this class of phenomena. First, we need to know what factors influence the selection of one perceptual interpretation over another, for knowledge of those factors could shed light on the extent to which the competition between alternative perceptual states is governed by low-level sensory features (sometimes called "bottom-up" factors) versus high-level cognitive interpretations (sometimes called "top-down" factors). And second, we would like to understand what causes perception to fluctuate when vision is faced with conflicting or ambiguous information. Why, in other words, does a given perceptual interpretation succumb to its competitor after only a few seconds of dominance, rather than persisting indefinitely? It is this second aspect of perceptual ambiguity—switching of dominance over time—that we examine in this paper.

One category of explanations of perceptual switching posits a process involving "satiation," whereby the neural activity associated with the currently dominant stimulus interpretation wanes in strength, eventually leading to restructuring of neural activity into a pattern supporting dominance of the alternative stimulus (Kohler, 1940). Consistent with this account, a number of studies have found that prolonged exposure, or adaptation, to an unambiguous version of a reversible stimulus biases observers to perceive the opposite configuration when viewing an ambiguous version of that stimulus immediately following adaptation (Long and Toppino, 1994; Harris, 1980; Hochberg, 1950; Nawrot and Blake, 1989; Long and Olszweski, 1999). Adaptation presumably weakens the neural responses underlying a given stimulus interpretation, temporarily tilting the balance of activity in favor of the neural representation not experienced during adaptation (Orbach et al., 1963; Kawamoto and Anderson, 1985). In the case of the KDE, satiation can be construed as the consequence of neural adaptation among disparity-selective neurons responsive to a given direction of motion (Nawrot and Blake, 1991a; Bradley et al., 1998). And in the case of binocular rivalry, satiation has been embodied in the form of neural adaptation of feature-specific neurons responsive to left-eye and right-eye rival figures (Lehky, 1988; Mueller, 1990; Wilson et al., 2001).

Besides satiation, there are several other alternative explanations of perceptual switching. According to one account, alternations in perception are a natural consequence of an adaptive sampling of possible perceptual interpretations, with sampling rate being autonomously driven by an intrinsic oscillator (Pettigrew, 2001). According to another account, high-level executive processes continuously guide and shape visual perception in the interests of current behavioral demands, and it is this interpretative process that is starkly revealed when one views rival figures or ambiguous stimuli (Hebb, 1958; Leopold and Logothetis, 1999). While not disputing the involvement of activity in lower-level, sensory visual ar-

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eas, this "interpretational" view envisions sensory activity being "steered and modified by central brain structures involved in planning and generating behavioral actions" (p. 254, Leopold and Logothetis, 1999). Evidence in support of this account includes the influence of global/meaningful context on binocular rivalry (Walker, 1978; Kovacs et al., 1997; Logothetis, 1998) as well as the existence of widespread neural activity in extrastriate visual areas and in frontalparietal regions at the time of spontaneous reversals in dominance during binocular rivalry (Lumer et al., 1998) and during viewing of ambiguous figures (Kleinschmidt et al., 1998).

One fruitful strategy for examining the possible causes of perceptual fluctuations is to identify conditions that affect the rate at which those fluctuations occur. Decades ago, Orbach et al. (1963) reported that spontaneous fluctuations in the perspective appearance of a Necker cube could be minimized by intermittent presentation of the inducing figure; indeed, under certain conditions of intermittency, the appearance of the Necker cube could be essentially stabilized such that no reversals in perception were experienced. In a recently published paper, Leopold and colleagues (Leopold et al., 2002) replicated this arresting phenomenon and showed that it generalizes to other forms of bistabililty, including KDE and binocular rivalry. Thus, for example, spontaneous fluctuations in perceived direction of rotation of a KDE globe were greatly reduced when the globe was intermittently visible; this stabilization of perception survived "off" periods lasting almost a minute. From these results, Leopold and colleagues concluded that bistability reveals the operation of high-level interpretative processes. Using a novel display procedure, we have discovered another equally potent strategy for significantly altering the dynamics of bistable perception. Specifically, binocular rivalry alternations can be substantially slowed—and sometimes completely arrested for over half a minute—when the rival targets are continuously visible but move around the visual field. Similarly, perceptual organization of an ambiguous KDE globe can be stabilized for extended periods by moving the component directions smoothly and continuously through "direction space." While not disproving the involvement of "high-level" influences in the resolution of perceptual ambiguity, these findings provide fresh evidence that neural adaptation may also play an important role in causing perceptual alternations.

Results

Binocular Rivalry

This first series of experiments measured the rate of alternations in binocular rivalry under several different stimulus conditions. During 2 min observation periods, observers maintained strict central fixation and used keyboard buttons to track binocular rivalry between a radial grating viewed by one eye and a circular grating viewed by the other (Figure 1A). On some trials, the rival targets moved smoothly in tandem around an imaginary circle centered on the fixation point, and on the remaining trials the targets remained stationary at a given location on the circumference of that circle. During the "movement" condition, the rival figures revolved around the virtual circle at 6 rpm (36 deg/s). Readers may compare rivalry alternations with moving versus stationary targets by navigating to http://www.psy.vanderbilt.edu/faculty/blake/rivalry/bistable.html. Among 13 observers tested, there were large individual differences in average rates of rivalry, as indicated by the scatter of data points in Figure 1B (each plotted point corresponds to alternation rates for a given observer). This range of individual differences in alternation rate is entirely characteristic of binocular rivalry and other forms of bistable perception (e.g., Pettigrew, 2001). Nonetheless, dominance durations for all individuals during the "moving" condition were typically quite long compared to their "stationary" durations, resulting in significantly reduced alternation rates when the rival targets moved. In fact, one observer experienced in rivalry but naive about the experiment's purpose aborted her first moving trial after about 45 s, mistakenly believing that a computer error had resulted in presentation of only one of two rival targets. Incidentally, the slowing of rivalry is not attributable to the simple, meaningless shapes of the two competing geometric forms—significantly slower alternation rates were also measured using moving rival targets consisting of a face viewed by one eye and a house viewed by the other (X symbols, Figure 1B). Moreover, the lower average rates of alternation are not simply the result of an initial, very long dominance duration followed by more or less normal alternations. Rather, alternation rate is slow throughout the entire viewing period, as evidenced by the results from a separate analysis showing that alternation rates during the first 30 s of the 2 min viewing period did not differ from alternation rates during the final 30 s.

It is reasonable to wonder to what extent this pattern of results varies with the rate of movement of the rival targets. Accordingly, we measured alternation rates for several speeds of motion of the rival targets (expressed in angular deg/s) ranging from 0 (i.e., stationary) to 36 deg/s. Results from those measurements are shown in Figure 1C, where it can be seen that alternation rate varies with speed, within a limited range. It is worth noting that when moving at a speed of 12 deg/s (which is 2 rpm) a given rival target takes more than 5 s to move through a distance equivalent to the diameter of the target (i.e., a distance sufficient to bring that target onto a completely unstimulated region of the retina); 5 s is considerably longer than the average duration of dominance for the three observers tested in this experiment when rival targets are stationary (average dominance duration = 3.3 s). But when the rival targets move at 36 deg/s, the rival targets move onto "fresh" unadapted retina in less than 2 s, a duration briefer than this average dominance duration with static targets. These numbers are consistent with the idea that movement of the rival targets serves to minimize the contribution of local retinal adaptation to reversals in perceptual state.

Rival target movement per se is not responsible for this pattern of results, as demonstrated by the results from two additional complementary experiments. In one experiment, observers used pursuit eye movements to track the rival targets as they moved around the virtual circle, thereby maintaining the images of the targets on approximately the same retinal locations throughout the viewing period. On other trials, the rival targets remained

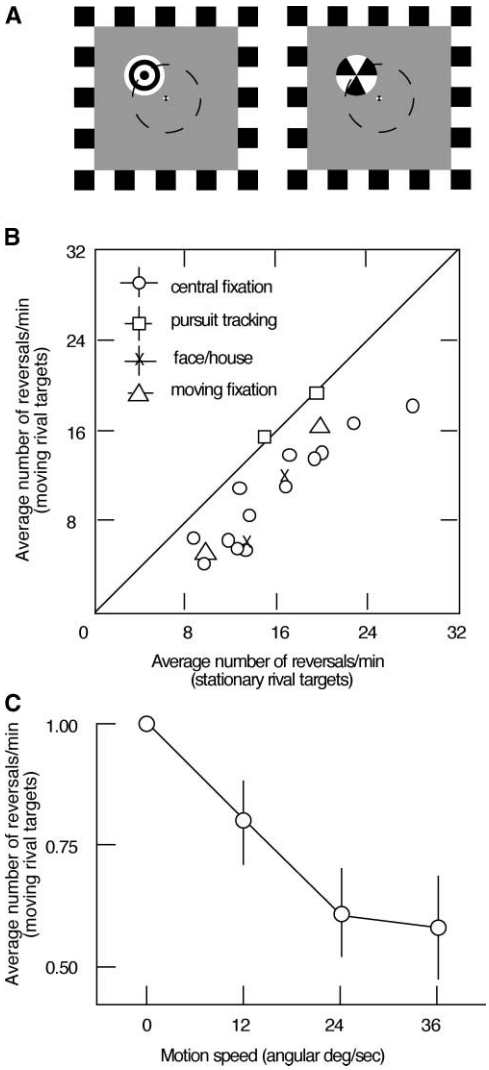

Figure 1. Moving versus Stationary Rivalry

(A) Schematic of rivalry displays. A bullseye viewed by one eye and a pinwheel viewed by the other always fell on corresponding retinal areas and, on some trials, this pair of rival figures moved in a circular trajectory (shown here as a dotted line, which was not present in the actual display) centered on a small fixation point located 0.44° from the center of the rival target.

(B) Alternation rate (number of transitions per minute, with each data point being the average of four 2 min tracking periods for a given observer, meaning that individual symbols of a given shape correspond to different observers). Circles: steady fixation on the central cross while targets either moved together around the virtual ring at the speed of 1 revolution/10 s (moving condition) or remained stationary in the upper left quadrant or lower right quadrant of the display throughout the 2 min tracking period; squares: steady fixation on the rival figures, thereby keeping those stimuli imaged on the fovea of both eyes, during trials where the figures either moved at 1 revolution/10 s around the circular path or remained stationary at one of two locations (upper left or lower right); X: steady fixation on a central cross while a picture of a house viewed by one eye and a picture of a face viewed by the other eye either moved in a circular path around the point of fixation (1 revolution/10 s) or remained stationary at one of two locations on the virtual circle (upper left or lower right quadrants); triangle: observers carefully moved their eyes to track a fixation point as it either moved around a pair of stationary rival figures (pinwheel and bullseye) located in the center of the display or remained stationary at a location above and to the left or below and to the right of the rival targets. The pairs of bars on the four symbols in the legend denote two times the average SEMs for alternation rates measured with moving targets (horizontal bar) and stationary targets (vertical bar).

(C) Alternation rate (number of transitions per minute, normalized to the alternation rate measured for the stationary condition) for rival targets whose speed of movement varied from 0 to 36 angular degrees/s. Four observers were tested in this experiment, and each individual's alternation rate averages were normalized by dividing those values by that individual's average alternation rate for the 0 deg/s condition (stationary), thereby taking into account individual differences in overall alternation rate. The vertical bars denote ±1 SEM.

stationary at a given location on the virtual circle, and observers simply fixated on those targets. For both conditions, observers tracked rivalry during 2 min viewing periods. Results from this experiment (open squares, Figure 1) reveal that alternation rates were *not* different for the moving and stationary conditions, presumably because the rival targets remained imaged on the same retinal location in both conditions. Movement per se, in other words, does not slow rivalry alternations. In the complementary experiment, the rival targets remained stationary in the center of the display and the small fixation mark either moved at 6 rpm around the virtual circle (motion condition) or remained stationary at a given location (stationary condition). During 2 min observation periods, the observer tracked rivalry between the rival targets while staring at the fixation point. Results from two observers tested on these two conditions (open triangles, Figure 1) show that rivalry rate was slowed for the motion condition (which caused the images of the rival targets to move in a circular path around the point of fixation) relative to the stationary condition (which maintained the images of the rival targets at a given retinal location). So, the critical stimulus condition for producing reduced alternations is movement of the image of the rival targets on the retina, not just movement of the targets around the visual field.

Do switches in rivalry state, when they do occur, tend to happen at a given location in their circular trajectory? For four observers, we repeated the rivalry alternation measurements using moving rival figures, this time always "tagging" the visual field location where each switch occurred. Each observer participated in four 2 min tracking periods, with the rival targets moving CW in half the periods and CCW in the other half. To analyze the results, we placed each switch location into one of 12 equal sized "bins" spaced evenly around the polar coordinates (a bin-width equivalent to 830 ms of travel around the circle). Inspection of those switch locations revealed large individual differences but no obvious tendency among all observers for these locations to be concentrated at given regions of the visual field (Figure 2). Significantly, for no observer did points congregate around the vertical meridian, as might be predicted if perceptual switching was associated with transitions from one hemisphere to another (Pettigrew, 2001).

In another experiment, we assessed the tendency for a given target to remain dominant under conditions in which both rival figures appeared to move beneath an occluding surface, thereby rendering both stimuli temporarily invisible (Figure 3). At the beginning of each trial, the pinwheel was situated directly to the right or

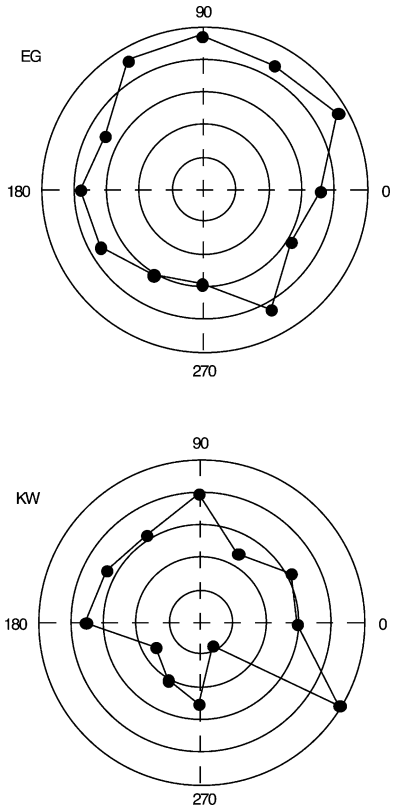

Figure 2. Transition Locations

Polar plots showing for two observers the distribution of locations in the visual field where transitions in rivalry occurred as the pair of rival targets moved around a circular path centered on the point of fixation. These data were obtained from trials on which the moving rival targets moved CW or moved CCW around the circular trajectory. The imaginary circle was subdivided into 12 equal-sized bins, and the incidence of reversals within each bin was tallied and plotted in polar coordinates. Among five observers tested, there was no general tendency for any given location to trigger reversals in perceptual state, and these two observers represent the extremes in the sample.

to the left of the fixation mark in one eye's display; the bullseye was situated at the same location in the other eye's display. While fixating on the middle of the display, observers monitored rivalry between the pinwheel and the bullseye and tapped the spacebar when a specified rival target achieved exclusive dominance. Trials were divided into two blocks, such that in one block the dominant stimulus was specified to be the bullseye and in the other block it was the pinwheel; the order of blocks was counterbalanced across observers. When the spacebar was tapped, the pair of rival targets began moving on a circular trajectory toward the top of the display. Midway around this trajectory the targets appeared to pass underneath an opaque occluder and then to reemerge on the other side; the vivid impression of occlusion was achieved by smooth deletion of portions of both rival targets, as if they were passing underneath the edge of a wedge-shaped, opaque surface whose color was identical to the background. The region of occlusion was wider than the rival targets, so both rival figures completely disappeared for approximately

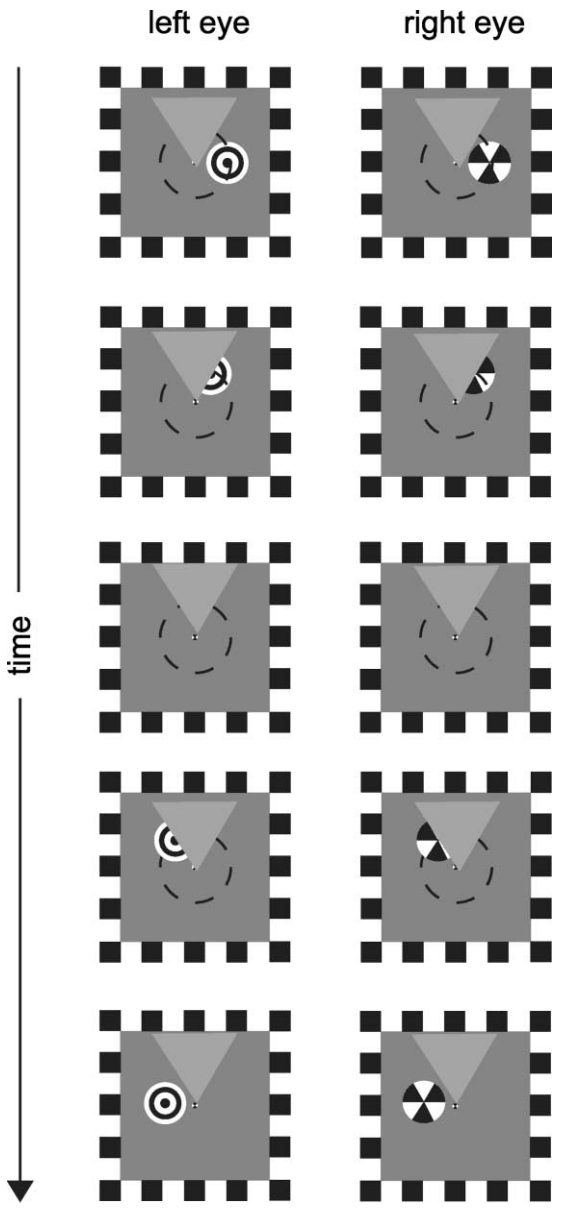

Figure 3. Occluded Rivalry

Schematic of sequence of events in an experiment where the pair of rival figures temporarily disappeared as they appeared to move behind a wedge-shaped occluding surface located at the top of the display (in the actual display the "wedge" region was the same color and luminance as the background region, with occlusion being depicted by continuous deletion and accretion of the rival targets). The pair of rival targets started their circular trajectory at either the lefthand or the righthand side of the display, with the observer initiating this movement when a given target was dominant in rivalry. Shortly after emerging from behind the occluder, the two rival targets were physically removed, and the observer indicated which target was dominant at that time. For purposes of comparison, an equal number of trials were administered in which the pair of rival targets moved in front of the occluder, thereby never disappearing.

1 s. The rival figures continued to move until both were again physically present in their entirety, at which point they both were extinguished. The observer reported the identity of the rival figure that was perceptually dominant

immediately after the pair completely reemerged from under the occluder. From these responses, we computed the probability of a switch in perceptual state during occlusion. We collected comparable responses on an equal number of trials where the rival targets never disappeared during their trajectory, which lasted the same duration as that associated with the occlusion condition. The probability of a switch in dominance was 0.18 when the rival targets remained continuously visible, which simply documents the relatively small likelihood that transitions will occur during movement. For trials on which the rival figures appeared to pass behind the occluder, the probability of a switch was 0.47. So, when the targets reappear in a location different from that associated with their disappearance, the initially visible target is just as likely to be the previously suppressed one as the one that had been dominant.

Thus, maintenance of rivalry dominance with movement does not survive the temporary disappearance of both targets. This observation stands in marked contrast to rivalry's behavior with stationary rival targets, where a given stimulus maintains dominance even when both rival figures are turned off for a short time and then turned on again (Leopold et al., 2002). We believe the key difference between these two situations has to do with whether or not the rival figures remain in the same location in the visual field during intermittent appearance. To test this conjecture, we measured the incidence of dominance switches under a condition where the rival targets themselves remained in the same retinal location before and after being temporarily occluded by a moving occluder (to envision this condition, simply reverse the roles of the occluders and the rival targets in Figure 3). The duration of disappearance was exactly the same as in the previous experiment, and the observer simply reported whether or not the dominant rival target before occlusion was the same as the dominant target immediately after occlusion. For this condition, the probability of a switch in dominance averaged 0.16, replicating the phenomenon documented by Leopold et al. (2002). So, we are confident that a crucial aspect of the "memory" effect reported by Leopold et al. is reappearance of the rival figures at the same location in the visual field. This same conclusion was reached by X. Chen and S. He (personal communication; reported at meetings of the Vision Sciences Society, 2003), using somewhat different procedures.

In the fourth and last rivalry experiment, we asked whether adaptation to one of two rival figures at a given region of the visual field would subsequently alter the pattern of rivalry alternations when rivalry moved into and through this localized region of adaptation. The sequence of events for a single trial is illustrated in Figure 4. The observer initially adapted to a high-contrast (80%) version of one of the rival figures located either directly to the left of fixation or directly to the right of fixation; the location of the adapting figure remained constant within a block of 20 trials, and over blocks of trials, this location was counterbalanced between "left" and "right" of fixation. The initial period of adaptation lasted 60 s and subsequent adaptation periods lasted 10 s, a "top-up" duration sufficient to maintain a constant level of adaptation. Throughout each trial, the observer always stared at the central fixation mark. At the

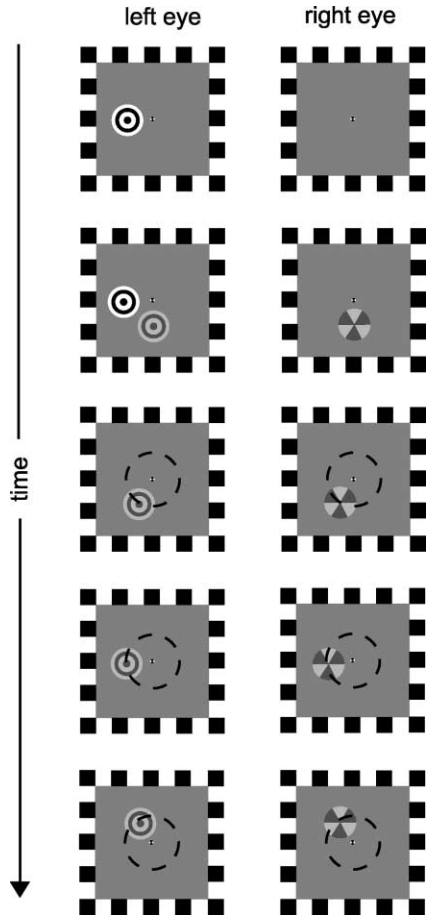

Figure 4. Adaptation and Rivalry

Schematic of a sequence of events in an experiment where circular trajectory of the pair of rivalry figures sometimes carried one of the figures onto a region of that eye's view that had been exposed to a high-contrast "adaptation" version of that figure (shown in this diagram as the bullseye). On other trials (not illustrated), the pair of rival targets moved in a trajectory away from the region of adaptation. For this experiment, the angular distance between the fixation cross and the center of the rival targets was 0.66°, and the width of the outer portion of the checkered border was 2.4°.

end of the adaptation period, two low-contrast (3%) rival figures appeared and remained directly below the fixation mark. The observer pressed and held the space bar when one of the two rival figures, designated for that block of trials, was dominant exclusively. When the space bar was pressed, the adaptation figure disappeared, and the pair of rival targets began moving smoothly around the virtual circle. On half of the trials, the trajectory of the rival figures carried them onto and through the region of the visual field previously exposed to the adaptation figure, and on the other half of the trials their trajectory carried them in the opposite direction away from the region of adaptation. Once the rival gratings had moved through 3/8 of a revolution (such that the figure was again outside the adapted region of the retina), they were extinguished. The observer was instructed to release the space bar when the initially dominant rival figure disappeared, and on each trial the computer recorded whether or not this key release oc-

curred before the figure moved through and beyond the boundaries of the adapted portion of the retina. Immediately following the observer's response, the 10 s "topping up" adaptation period commenced.

Results from this experiment consisted of the proportion of trials for which a transition in state occurred prior to the end of the trial for three categories of trials: (1) initially dominant figure moves along a trajectory that brings it within a region of the visual field adapted to that figure, (2) initially dominant figure moves along a trajectory that brings it within a region of the visual field adapted to the other rival figure, and (3) initially dominant figure moves along a trajectory that moves it away from the adapted region of the visual field. For both observers tested, the incidence of disappearance of the figure falling within the adapted region (condition 1) was quite high when that figure was identical in form to the adapting figure (85% and 80% for observers R.B. and D.B., respectively); when the nonadapted figure moved into the adapted region (condition 2), transitions were infrequent (15% and 20%) as were transitions when the rival target moved into the opposite nonadapted portion of the visual field (condition 3; 15% and 20%). Thus, we conclude that the prolongation of dominance of a rival figure promoted by motion of that figure can be counteracted by moving that dominant rival figure into a region of the visual field adapted to a high-contrast version of that figure.

From other work, we know that pattern adaptation reduces the effective contrast of a subsequently viewed test pattern when test and adaptation patterns fall on the same retinal area (Blakemore et al., 1973). For a variety of reasons, it is thought that this adaptation effect is attributable to the temporary reduction in responsiveness of neurons at early stages of visual processing (Blakemore and Campbell, 1969; De Valois and De Valois, 1988; Graham, 1989). Moreover, it is known that this reduction in effective contrast influences the dynamics of binocular rivalry (Blake et al., 1979). By demonstrating that the effect of adaptation generalizes to rival figures that move temporarily into a region of adapted retina, the present results imply that the frequent disappearance of a dominant rival figure is caused by the weakening of neural signals associated with that figure. This weakening can be induced by moving a rival figure onto an adapted region of the retina or, presumably, by leaving that figure at the same retinal area, thereby triggering a process of self-adaptation (Kawamoto and Anderson, 1985). It should be noted that this conclusion deals with the question of perceptual alternations and has no necessary bearing on the issue of whether rivalry is based on interocular competition (Blake, 1989) or high-level stimulus representations (Logothetis et al., 1996).

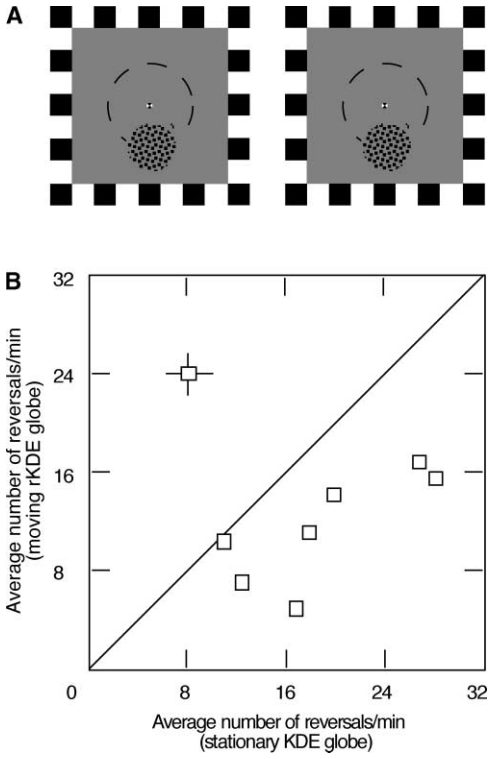

Figure 5. Moving versus Stationary Globe

(A) Schematic of rotating globe display.

(B) Alternation rate (number of transitions per minute, with each data point being the average of four 2 min tracking periods for a given observer, meaning that different symbols correspond to different observers) measured on trials where the globe moved around the point of fixation (movement condition) and on trials where the rotating globe remained at the same location on the virtual circle (upper left or lower right). The pair of bars on the symbol in the legend denotes two times the average SEMs for the rate of alternation in perceived direction of rotation.

Ambiguous Motion

Are other forms of bistable perception comparably stabilized when those figures undergo changes designed to preclude self-adaptation? To answer this question, we turned to the reversible KDE globe whose direction of rotation is ambiguous and, therefore, bistable (Nawrot and Blake, 1991b). Specifically, we measured alternations in perceived direction of rotation of a "globe," defined by 100 dots moving in a manner simulating rotation about the vertical axis; both eyes viewed the same image (binocular rivalry did not occur). Because the optic flow defining the globe is consistent with either direction of rotation, observers experience spontaneous reversals in rotational direction over time, and these reversals are easily tracked by pressing keys. As in the case of rivalry, moving the ambiguous globe steadily around the point of fixation significantly slowed—but did not arrest—alternations in perceived direction of motion (Figure 5). Again, we are tempted to attribute this slowing effect to a retardation in the build up of neural adaptation at a given location of the visual field. Presumably, the stationary globe produces prolonged neural activation of populations of visual neurons each selectively responsive to one of the two directions of motion contained in the KDE stimulus. Moving the globe around the visual field would, therefore, continuously shift that stimulus into the receptive fields of unadapted neurons.

If this conjecture is correct, we would predict that other manipulations designed to promote the engagement of unadapted neurons during extended viewing should retard reversals in perceived direction of rotation

of the KDE globe. In a final experiment, we tested this prediction using an entirely different strategy for minimizing the contribution of local neural adaptation to the motion vectors defining the ambiguous globe. As a reminder, the ambiguous kinetic globe is defined by dots moving transparently in opposite directions (at any given moment, half are moving leftward and half are moving rightward). With that in mind, we reasoned that continuously varying the mean direction of those opponent motion vectors should reduce the effects of adaptation at any given direction of motion and, therefore, slow fluctuations in the globe's configuration. Accordingly, we had observers track changes in direction of rotation of a KDE globe whose angular degree of "wobble" centered on the vertical axis was varied randomly from trial to trial. The globe itself remained at the same visual field location, and observers fixated the center of the globe while tracking the two alternative directions of rotation during 1 min observation periods.

All five observers showed the same pattern of results (Figure 6): a reduction in alternation rate with increasing degrees of wobble around the vertical axis. This fall off in alternation rate was not caused by uncertainty in perceived direction of rotation at the larger ranges of angular shift—observers reported no difficulty judging when perceived direction of rotation reversed. Readers may confirm this observation by viewing the animations provided at http://www.psy.vanderbilt.edu/faculty/blake/rivalry/bistable.html.

Could the slowing of reversal rate of the ambiguous globe be attributable to the particular directions of motion engaged with increasing angular deviations from vertical? There is some evidence that signals associated with oblique directions of motion are less effective than those associated with cardinal directions, although this anisotropy is very weak (Gros et al., 1998). To determine whether the results in Figure 6 are peculiar to directional variations about the vertical axis, we repeated this entire experiment on two observers, now centering the continuously changing directions of motion around an axis that was rotated 45° CCW from vertical. In all other respects, the procedures were the same, and the same pattern of results was obtained (open symbols, Figure 6). We are confident, therefore, that the slowing of alternation rate is caused by the continuous change in directions of motion defining the ambiguous KDE globe.

Discussion

In several experiments, we find that conflicting figures and ambiguous motion sequences undergo slower rates of perceptual alternation when those stimuli move continuously around the visual field. Converging lines of evidence lead us to conclude that continuous movement of these visual figures reduces the build up of local neural adaptation, which itself is involved in the dynamics of perceptual reversals. Of course, our account leaves unexplained just why a given perceptual interpretation persists as the evoking stimulus moves around the visual field and, therefore, engages ever-changing, fresh neural machinery. What is responsible for the memory-like process implied by the persistence of a given perceptual interpretation? Perhaps the underlying neural circuitry in visual cortex promotes perceptual persistence. After all, we know that neurons representing adjacent regions of the visual field are richly interconnected in ways that promote synergistic neural interactions among those neurons activated by similar stimulus features (Gilbert, 1992). Thus, when a given figure or stimulus interpretation is currently dominant, the neural activity associated with that figure could conceivably "prime" activity among neighboring neurons soon to be directly activated when that stimulus moves into their receptive fields. Alternatively, it is also possible that movement—itself being a potent grouping cue—reinforces a given perceptual interpretation and, thereby, promotes its continued visibility. Whatever force promotes maintenance of perceptual dominance, it appears to be susceptible to temporary removal of the rival stimuli, as shown by the occlusion experiment (Figure 3).

The conclusion advanced here—movement minimizes local neural adaptation and, therefore, retards perceptual switching—does not rule out the involvement of high-level brain areas operating in an "interpretive" mode to influence the dynamics of perception when viewing conflicting or ambiguous stimuli (Andrews and Purves, 1997; Leopold et al., 2002). Indeed, in the case of rivalry, such top-down influences are to be expected because the dominance phases of rivalry are equivalent in all respects to vision during normal monocular viewing (Blake, 2001). Hence, whatever top-down processes operate during ordinary vision should be triggered by a dominant stimulus. All evidence indicates, however, that a stimulus temporarily suppressed during rivalry is functionally blocked from higher visual areas, rendering it completely ineffective in all but the most rudimentary aspects of visual processing. Eventually, however, the suppressed stimulus does achieve perceptual dominance, in no small part because of the neural adaptation associated with the currently dominant stimulus.

How do the present results square with the findings and ideas of Leopold and colleagues (Leopold et al., 2002)? For several bistable phenomena, they showed that perceptual alternations could be slowed considerably by periodic removal of the stimulus from perceptual awareness. For this procedure to work, of course, the durations of intermittent stimulus exposure needed to be shorter than the average duration of dominance of a given perceptual state. Leopold and colleagues believe the recurrence of the same perceptual state with intermittent exposure is indicative of some form of perceptual memory that can survive for many seconds in the absence of perceptual experience. Translating this idea into neural terms, one could construe this behavior as a form of hysteresis wherein the current neural representation of a perceptual state is determined both by the present state of stimulation and by the prior history of stimulation. As Wilson (1999) among others has pointed out, hysteresis is a common property of neural networks whose excitatory and inhibitory interactions promote multiple stable states. Fluctuations in activity states within such a network can be driven by self-adaptation, wherein the response strength of the currently active state steadily weakens with time. Adaptation leads to switches in state, with the dynamics affected by the time constant of adaptation. Viewed in this light, the results reported in this paper imply that

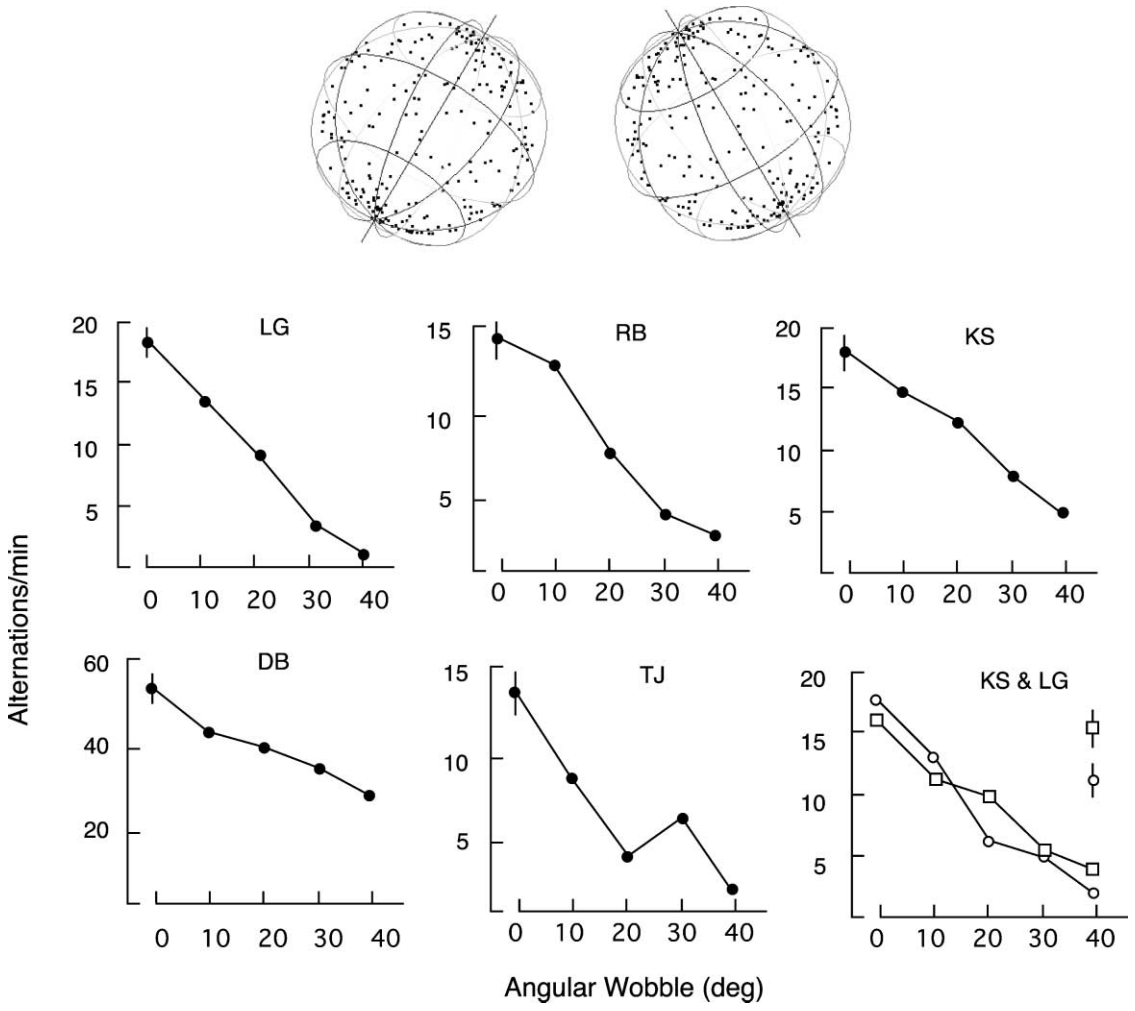

Figure 6. Wobbling Globe

(A) Schematic showing two frames (nonconsecutive) from an animation sequence depicting a dot-defined globe whose axis of rotation changed continuously over time. In the animations themselves, only the dots defining the motion vectors appeared, yielding the compelling impression of a globe revolving about its axis of rotation, which itself was "wobbling" over time. A QuickTime© animation illustrating two different degrees of "wobble" may be viewed by navigating to http://www.psy.vanderbilt.edu/faculty/blake/rivalry/bistable.html.

(B) Two naive individuals and the three authors, all with normal or corrected-to-normal vision, served as observers. Each observer completed four repetitions for each value of angular displacement (order randomized within and between observers) resulting in a total of 20 trials. On each 60 s trial, observers tracked the direction of rotation of the globe (CW or CCW) and recorded their responses via keypress. Vertical bars for the 0 wobble condition in each plot denote two times the average SEM for all conditions for that observer.

minimizing the build up of adaptation increases the time between perceptual transitions. Indeed, there is nothing about our results or, to our knowledge, the results of Leopold and colleagues that is inconsistent with this characterization of perceptual reversals during rivalry and during viewing of bistable stimuli.

Whatever the bases for perceptual alternations, our novel procedure involving movement of an ambiguous or conflicting stimulus around visual space (or around "direction" space) offers a potent means for temporarily stabilizing the brain's response when faced with perceptual conflict. This stabilizing influence could be particularly valuable when attempting to study the neural concomitants of perceptual ambiguity using brain imaging techniques (Lumer et al., 1998; Kleinschmidt et al., 1998; Tong et al., 1998; Polonsky et al., 2000).

Experimental Procedures

Binocular Rivalry

Dichoptic rival displays, shown schematically in Figure 1, were generated under computer control on the two halves of a color video monitor (frame rate 75 Hz) viewed through a mirror stereoscope. Rival figures comprised a radial grating ("pinwheel") viewed by one eye and a circular grating ("bullseye") viewed by the other; each rival figure subtended 0.55° visual angle, and the contrast of each was 50% unless otherwise specified. A 2.4° square checkered border surrounding each rival figure served to maintain the eyes at a convergence angle appropriate for the viewing distance. Prior to each test session, the observer carefully adjusted the mirrors of the stereoscope to achieve stable binocular alignment. The gray background luminance of the video monitor (16 cd m^{-2}) provided the only illumination within the otherwise dark test room.

For all experiments, the observer fixated on a small, central cross (6.6 arc min) and pressed keys on the computer keyboard to indicate which rival figure—pinwheel or bullseye—was dominant at any given

moment. Observers were instructed to press neither key when experiencing mixed dominance characterized by simultaneous perception of portions of both rival figures. (With these small rival figures, mixed dominance was experienced very infrequently.) For all experiments, a given rival figure was presented to the left eye on some trials and to the right eye on other trials, with the order of presentations being random. For several experiments, observers tracked rivalry continuously during extended viewing periods. For other experiments, observers were administered discrete trials initiated contingent on the dominance of a given rival target.

Ambiguous Kinetic Globe

These animations comprised 2D random-dot cinematograms created by the parallel projection of a mathematically defined 3D sphere. Each frame of the cinematogram consisted of 100 small (1.6×1.6 min) white dots representing random points on the surface of a 3D sphere with a diameter of 1.1° (dot luminance = 63.43 cd/m^{-2}; background luminance = 6.00 cd/m^{-2}). Each dot's position was updated from frame to frame (frame duration = 8.33 ms), thereby creating the perception of smooth, continuous motion of a sphere in 3D space. In every condition, the sphere rotated about its central axis at a rate of 15 rpm, and on movement trials the entire globe rotated about the virtual circle centered on the fixation mark at 6 rpm.

For the "wobble" experiment, the sphere was composed of 240 dots and its diameter was 4.2°. In addition to rotating about its vertical axis at 15 rpm, the KDE sphere's axis of rotation also varied about a given angle at a rate of 7.5 rpm (see Figure 6). The angle of rotation was either 0° (no displacement), 10°, 20°, 30°, or 40°.

Observers

All experiments included both naive and experienced psychophysical observers (including the authors). All observers have normal or corrected-to-normal acuity and good stereopsis. The experiments were approved by the Institutional Review Board of Vanderbilt University.

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