Neuron
Article

Long-Term Speeding in Perceptual Switches Mediated by Attention-Dependent Plasticity in Cortical Visual Processing

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DOI 10.1016/j.neuron.2007.09.028

SUMMARY

Binocular rivalry has been extensively studied to understand the mechanisms that control switches in visual awareness and much has been revealed about the contributions of stimulus and cognitive factors. Because visual processes are fundamentally adaptive, however, it is also important to understand how experience alters the dynamics of perceptual switches. When observers viewed binocular rivalry repeatedly over many days, the rate of perceptual switches increased as much as 3-fold. This long-term rivalry speeding exhibited a pattern of image-feature specificity that ruled out primary contributions from strategic and nonsensory factors and implicated neural plasticity occurring in both low- and high-level visual processes in the ventral stream. Furthermore, the speeding occurred only when the rivaling patterns were voluntarily attended, suggesting that the underlying neural plasticity selectively engages when stimuli are behaviorally relevant. Long-term rivalry speeding may thus reflect broader mechanisms that facilitate quick assessments of signals that contain multiple behaviorally relevant interpretations.

INTRODUCTION

When visual input allows for multiple coherent interpretations, the visual system normally selects one interpretation at a time. For example, the appearance of a square array of dots spontaneously changes among several interpretations: rows, columns, diagonals, and so on. Switches in perceptual interpretations are more dramatic in cleverly designed bistable (or multistable) figures such as Rubin's face-vase, the Necker cube, and an apparent-motion quartet, all of which exhibit two or more impressively distinct interpretations (e.g., Attneave, 1971). Binocular rivalry is a strong and versatile case of such perceptual multistability. It is strong in that when one image predominates, the competing image is often completely invisible. It is versatile in that any pair of sufficiently different (i.e., nonfusible) patterns presented dichoptically can generate exclusive perceptual switches. Binocular rivalry has thus been extensively used as a laboratory paradigm to understand the mechanisms that spontaneously bring alternative sensory interpretations into awareness (see Blake and Logothetis, 2002; Alais and Blake, 2005, and Tong et al., 2006, for recent reviews).

Neuroscientific evidence suggests that binocular rivalry for static images involves neural competition occurring in multiple visual areas throughout the ventral stream (V1, V2, V4 through IT, thought to process visual objects; e.g., Sheinberg and Logothetis, 1997; Logothetis, 1998; Polonsky et al., 2000; Tong and Engel, 2001; Fang and He, 2005; see Leopold and Logothetis, 1999; Blake and Logothetis, 2002; Suzuki and Grabowecky, 2002a, and Tong et al., 2006, for reviews). Single-cell recording and computational results (but not fMRI results) further suggest that neural competition builds up so that the competition becomes stronger in higher visual areas (e.g., Leopold and Logothetis, 1999; Wilson, 2003; Freeman, 2005; Tong et al., 2006). Behavioral results are overall consistent with this idea of cascading multilevel neural competition mediating perceptual switches in binocular rivalry. For example, perceptual suppression during binocular rivalry is stronger for features that are thought to be coded in higher visual areas (e.g., Nguyen et al., 2003), perceptual suppression reduces both low-level and high-level visual aftereffects but more strongly reduces high-level aftereffects (e.g., Cave et al., 1998; Moradi et al., 2005; Blake et al., 2006), and perceptual rivalry becomes stronger (i.e., more mutually exclusive) when the stimuli are designed to induce competition in additional feature processing (e.g., perceptual rivalry becomes stronger from orientation-based competition to orientation-and-color-based competition to orientation-and-color-and-eye-based competition; Campbell and Howell, 1972; Campbell et al., 1973; Wade, 1975). In addition to these results suggesting contributions from multilevel neural competition to binocular rivalry, numerous other studies have determined how the dynamics of binocular rivalry are influenced by the characteristics of the competing patterns, such as their contrast, contour density, grouping, motion, and familiarity (see Blake and

Logothetis, 2002; Alais and Blake, 2005, and Tong et al., 2006, for reviews).

Relatively few studies, however, have investigated how binocular rivalry depends on perceptual experience. Most of them examined effects of pattern preadaptation, with the general conclusion that a minute or so of pattern previewing reduces the dominance duration of the adapted pattern in subsequent binocular rivalry. This effect is generally attributed to activation-based desensitization of visual neurons that preferentially respond to the adaptor pattern (e.g., Blake and Overton, 1979; Blake et al., 1980, 2003; Suzuki and Grabowecky, 2003). Pattern adaptation also occurs in the course of experiencing binocular rivalry, effectively reducing the contrast of the competing patterns. Because binocular rivalry is slowed when the competing patterns are reduced in contrast (e.g., Levelt, 1965), the build up of contrast adaptation to the competing patterns should gradually slow binocular rivalry, and this has been verified (e.g., Lehky, 1995; van Ee, 2005; also see Suzuki and Grabowecky, 2002b, for a related result in multistable binocular rivalry).

In addition to this short-term slowing, there have been anecdotal reports that individuals who have experienced many hours and days of binocular rivalry tend to exhibit faster perceptual switching. No studies, however, have systematically investigated the effects of long-term experience on the dynamics of perceptual switches in binocular rivalry. The time course, underlying neural mechanisms, and potential behavioral relevance of long-term plasticity in perceptual switching are thus unknown. The goal of the current study was 3-fold: (1) to systematically determine the time course of plasticity in the dynamics of binocular rivalry, including a demonstration of substantial long-term speeding, (2) to elucidate the underlying neural substrate of this long-term rivalry speeding by characterizing its specificity for image features, and (3) to evaluate the potential behavioral relevance of long-term rivalry speeding by manipulating attention toward or away from the rivaling stimuli.

Determining the Time Course of Plasticity in Binocular Rivalry

We examined changes in the rate of perceptual switches over three time scales: (1) during a 20 s period of continuously viewing binocular rivalry (we call this a *trial*), (2) over repeated trials with short intervals between them (we call this a *session*), and (3) over repeated sessions with long intervals between them. We expected to replicate short-term slowing of binocular rivalry during each trial (e.g., Lehky, 1995; van Ee, 2005). We also expected to replicate a stable rate of binocular rivalry over a session (e.g., van Ee, 2005) when sufficient time (~3 min) was given between trials for recovery from contrast adaptation (Albrecht et al., 1984). To determine the time course and extent of long-term speeding of perceptual switches in binocular rivalry, we administered multiple (14–40) sessions, with intersession intervals averaging 1.7 days.

Elucidating the Neural Loci of Plasticity Underlying Long-Term Rivalry Speeding

Broadly, two potential mechanisms could mediate long-term rivalry speeding. Long-term rivalry speeding could be due to general nonsensory factors such as increased instability in eye fixation (van Dam and van Ee, 2006), increased arousal (e.g., George, 1936), increased voluntary attention (Paffen et al., 2007), an increased intentional effort to speed perceptual switches (e.g., Lack, 1974, 1978; Meng and Tong, 2004; van Ee et al., 2005), or a combination of these factors (potentially mediated by feedback signals from frontal and prefrontal cortexes; e.g., Nagahama et al., 1998; Hauser, 1999; Lumer and Rees, 1999; Kastner and Ungerleider, 2001; Armstrong et al., 2006; see Duncan, 2001, and Miller and Cohen, 2001, for reviews). Long-term rivalry speeding could also be mediated by plasticity in visual processes, where the loci of plasticity could involve low-level processing, high-level processing, or both.

Our goal was to determine the extent to which plasticity in different stages of visual processing and nonsensory factors contribute to long-term rivalry speeding. We accomplished this by using a "transfer" paradigm similar to that often employed in perceptual learning studies (e.g., Fiorentini and Berardi, 1980; Ball and Sekuler, 1982; Karni and Sagi, 1991; see Suzuki and Goolsby, 2003; Fahle, 2004, and Ahissar and Hochstein, 2004, for reviews). The logic is that if rivalry speeding is mediated by plasticity involving visual neurons that respond selectively to feature *X* (e.g., selective for position), the speeding due to long-term experience should be eliminated when feature *X* is changed (e.g., when the stimulus position is changed). In contrast, if the long-term speeding is mediated by plasticity involving visual neurons that are invariant for feature *X* (e.g., invariant for position), the speeding should persist even when feature *X* is altered. We evaluated the transfer of long-term rivalry speeding with respect to a variety of image features that are coded in different levels of ventral visual processing (thought to mediate perceptual rivalry for static images; see above). Specifically, we manipulated (1) "low-level" features that are primarily coded in low-level processing, (2) "multilevel" features that are coded in both low- and high-level processing, and (3) component parts that are coded (distinctly from the whole shape to which they belong) in high-level processing. In this way, we were able to evaluate the roles of plasticity occurring in different levels of visual processing.

Our manipulations of low-level features included changes in fine-scale position, fine-scale orientation, and eye of origin (the eye to which each pattern was presented). The 0.42° position shifts that we used should be resolved in V1 with small neural receptive fields (~0.3° at our stimulus eccentricity of 0.65°), but unresolved in higher visual areas with larger receptive fields (~1°–4° in V4, ~5° in TEO, and ~2.5°–40° in TE at our stimulus eccentricity) (e.g., Hubel and Wiesel, 1974; Schiller et al., 1976b; Dow et al., 1981; Desimone and Schein, 1987; Boussaoud et al., 1991; Kastner et al., 2001; DiCarlo and

Maunsell, 2003). The 23° orientation change that we used is substantial with respect to neural orientation tuning in V1 (with tuning bandwidths of 25°–40°), but relatively minor with respect to coarser orientation tuning in higher visual areas (with tuning bandwidths of ~58° in V2, 36°–75° in V4, and ~70° in IT) (e.g., Schiller et al., 1976b; Desimone and Schein, 1987; Levitt et al., 1994; Vogels and Orban, 1994; Geisler and Albrecht, 1997; McAdams and Maunsell, 1999). Eye preferences are strong in V1 but diminish in higher visual areas, and most neurons in IT show no eye preference (e.g., Hubel and Wiesel, 1965, 1968a, 1968b; Gross et al., 1972; Uka et al., 2000; Watanabe et al., 2002a). Thus, our manipulations of fine-scale position, fine-scale orientation, and eye of origin primarily affected low-level visual processing.

Our manipulations of multilevel features included changes in visual hemifield (left or right) and contrast polarity (dark or light against the background). Receptive fields of neurons throughout the ventral visual stream (from V1, V2, V4 through IT) are confined within the contralateral visual hemifield (except for some neurons in the highest area TE) (e.g., Desimone and Gross, 1979; Boussaoud et al., 1991; Kastner et al., 2001; DiCarlo and Maunsell, 2003). A substantial proportion of neurons in each ventral visual area also exhibit preferences for contrast polarity (e.g., Hubel and Wiesel, 1968a; Desimone and Schein, 1987; Ito et al., 1994; Levitt et al., 1994; George et al., 1999). Thus, visual hemifield and contrast polarity are coded throughout multiple visual areas in the ventral stream.

Finally, high-level visual neurons in the ventral stream are selective for global shapes so that they tend not to respond to isolated parts of their preferred patterns (e.g., Hikosaka, 1999; Tanaka, 1996). In contrast, low-level visual neurons respond to their preferred local oriented edges relatively independently of the global shape to which the edges belong (though their responses are modulated by visual contexts beyond the extent of their classical receptive fields; e.g., Zipser et al., 1996; Lamme et al., 1999; Nothdurft et al., 1999). Thus, the whole shape and their component parts are distinctly coded primarily in high-level visual areas.

These feature manipulations allowed us to evaluate how nonsensory factors and plasticity in low- and high-level visual processes contribute to long-term rivalry speeding. For example, substantial specificity of long-term rivalry speeding obtained for any image feature would implicate plasticity involving visual processing, thereby ruling out the possibility that the speeding might be all due to nonsensory factors. Complete specificity (no transfer) obtained for any image feature would rule out contributions from any processes that are stimulus nonspecific. Furthermore, specificity obtained for eye of origin would indicate that the underlying plasticity extends to processing of visual features that are not consciously available, as people are normally unaware of the eye-of-origin information (e.g., Ono and Barbeito, 1985).

Importantly, the overall pattern of feature specificity would elucidate which visual areas contribute to long-term rivalry speeding. If the speeding involves plasticity in low-level visual processing, it should be specific for all features that are coded in low-level visual areas (fine-scale position, fine-scale orientation, eye of origin, visual hemifield, and contrast polarity) and should transfer to component parts (because the local edge features of the parts were subsumed in the whole pattern for our stimuli). If the speeding is primarily mediated by plasticity in high-level processing, it should be specific for features that are coded in high-level visual areas (visual hemifield and contrast polarity), nonspecific for features that are primarily coded in low-level visual areas (fine-scale position, fine-scale orientation, and eye of origin), and should not transfer to component parts. If neural plasticity in both low- and high-level visual processing contributes to long-term rivalry speeding, the speeding should be most specific for features that are coded across multiple visual areas (visual hemifield and contrast polarity), moderately but substantially specific for features that are primarily coded in low-level visual areas (fine-scale position, fine-scale orientation, and eye of origin), and should partially transfer to component parts (due to contributions from low-level processing).

Examining the Potential Behavioral Relevance of Long-Term Rivalry Speeding

Whereas our first two aims were to characterize the time course of long-term plasticity in perceptual switches and to elucidate the underlying neural substrate of this plasticity, our third aim was to examine the potential behavioral relevance of long-term rivalry speeding. One way to address behavioral relevance is to manipulate attention. Our rationale was as follows. If long-term rivalry speeding occurs only when observers voluntarily attend to the competing stimuli, such a result would suggest that the rate of perceiving alternative percepts becomes faster only for attended and thus behaviorally relevant aspects of the stimulus environment. This in turn would suggest that long-term speeding in perceptual switches potentially plays a functional role by allowing an organism to quickly examine behaviorally relevant alternative interpretations from a frequently encountered visual scene.

RESULTS

Our standard rivalry stimulus consisted of a "+"and an "x" shape presented dichoptically (i.e., each shape presented to a different eye; Figure 1). We chose these shapes because (1) they are familiar and easily identifiable shapes composed of simple rectangular parts, and (2) they are likely to activate both low-level (due to their high-contrast oriented edges) and high-level (e.g., Sato et al., 1980; Hikosaka, 1999) visual processes.

We measured the speed of perceptual switches in terms of perceptual dominance durations (i.e., lengths of continuous perception of each shape) using a standard procedure (see the Experimental Procedures). We then analyzed the rates of perceptual switches (i.e., the

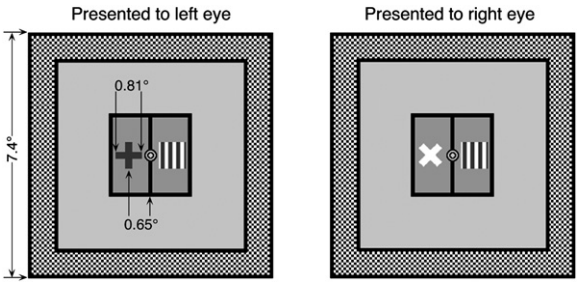

Figure 1. An Example of the Display Used to Induce Binocular Rivalry

The two images were presented dichoptically using a stereoscope consisting of four front-surface mirrors and a central divider. The high-contrast textured frames were binocularly presented around the rivaling shapes to facilitate stable binocular alignment. Perception spontaneously alternated between "+" and "x" shapes. A grating was presented binocularly on the opposite side to balance the overall stimulus configuration to help stabilize central fixation at the bull's-eye fixation marker.

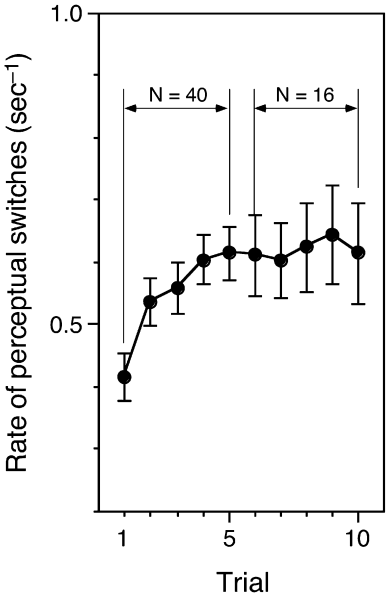

Figure 2. The Rapid Initial Speeding of Perceptual Switching within the First Several Trials of Experiencing Binocular Rivalry

The error bars indicate ±1 SEM, using observers as the random effect. For all 40 observers, the initial speeding was measured for five consecutive trials. For 16 of the 40 observers, the initial speeding was measured for ten consecutive trials (resulting in larger error bars for trials 6 through 10).

reciprocal of perceptual dominance durations). We used the rate scale because (1) the underlying neural mechanisms of perceptual switches seem to be more directly reflected in the rate scale than in the duration scale (e.g., Brascamp et al., 2005), and (2) the variability is nearly constant in the rate scale across a broad range of switching rates (see the first five trials in Figure 2, and Figures 4 and 6), thus providing an appropriate variable for parametric statistical analyses (note that reciprocally transforming the mean rates reported here will provide the corresponding harmonic means of dominance durations).

The Time Course of Plasticity in Binocular Rivalry

When an observer viewed binocular rivalry for the first time, initial perceptual switches were often very slow. Perceptual switches, however, quickly speeded within several trials to asymptote at a relatively stable rate (Figure 2).

Following this rapid initial speeding, experience-based plasticity in the dynamics of binocular rivalry was characterized by the three basic stages illustrated in Figure 3. First, rivalry gradually slowed in the course of each 20 s trial (illustrated in Figure 3 by the slanted lines). Second, the average rate of perceptual switches remained relatively constant over a session of 20 consecutive trials given with ~3 min intertrial intervals (illustrated in Figure 3 by the constant level of the slanted lines across repeated trials within each session). Third, in spite of this stability over massed trials, rivalry steadily speeded across sessions that were separated by an average of 1.7 days (illustrated in Figure 3 by the groups of slanted lines ascending across sessions). Experience-based plasticity in binocular rivalry is thus characterized by an initial rapid speeding (Figure 2) followed by within-trial slowing, within-session stability, and across-session speeding (Figure 3).

To quantify the within-trial slowing, for each trial for each observer (BK, LI, MG, ES, KS, TS, and PL), we computed the slope of linear correlation between the onset time of each perceptual dominance and the reciprocal duration of that dominance. A negative slope would indicate within-trial slowing in perceptual switches, whereas a positive slope would indicate within-trial speeding. We computed the slope as the total linear change per trial to illustrate the extent to which the rate of perceptual switches changed from the beginning to the end of each trial. The slope (averaged across all trials) was significantly negative ($M = -0.41$, SEM = 0.024, $d = 6.43$, $t_6 = -17.02$, $p < 0.0001$), indicating that binocular rivalry slowed within each trial.

To quantify the within-session stability, for each session for each observer (BK, LI, MG, ES, KS, TS, and PL), we computed the slope of linear correlation between the trial number (1 through 20) and the corresponding trials' average rate of perceptual switches. We computed the slope as the total linear change per session to illustrate the extent to which the average rate of perceptual switches changed from the 1st trial to the 20th trial. The slopes (averaged across all sessions) did not differ significantly from zero ($M = -0.0011$, SEM = 0.020, $d = 0.021$, $t_6 = -0.055$, *n.s.*), indicating that binocular rivalry was stable across trials within each session.

In contrast to this stability across massed trials within each session, binocular rivalry steadily and substantially speeded across sessions for each observer (BK, LI, MG, ES, KS, TS, and PL; see Figure 4). To determine whether this substantial speeding was accompanied by a change in the shape of the distribution of perceptual switching

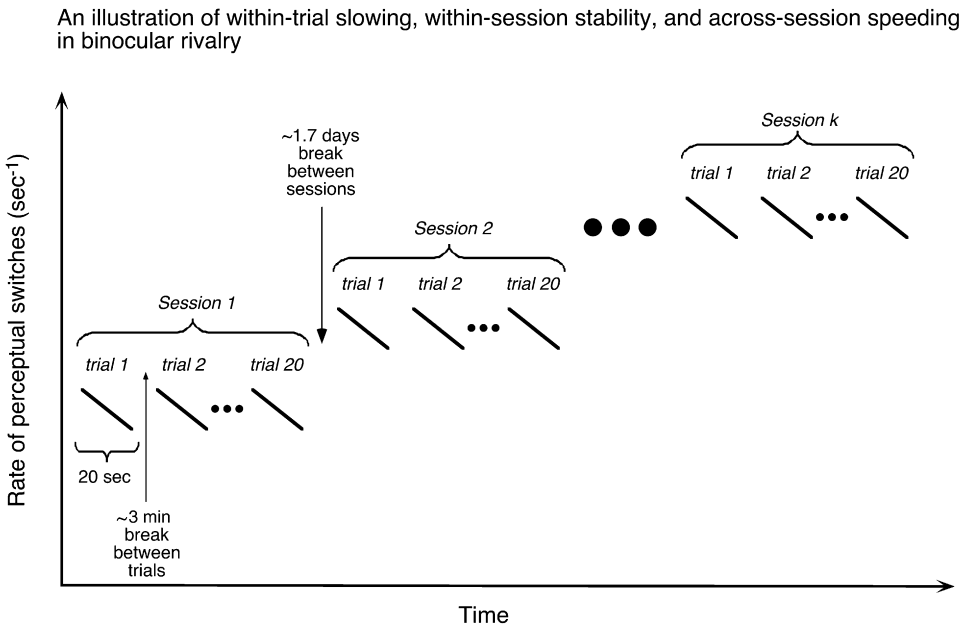

Figure 3. A Schematic Illustration of the Time Course of Long-Term Plasticity in Binocular Rivalry following the Initial Rapid Speeding

Each slanted line indicates that binocular rivalry gradually slowed within a 20 s trial. The fact that the slanted lines remain at the same level within each session indicates that the average rate of binocular rivalry was stable across multiple consecutive trials. When a session was repeated after a long interval, however, rivalry often substantially speeded (e.g., the slanted lines for session 2 are higher than those for session 1).

rates, we compared the normalized distributions of switching rates (the data for each session from each observer were divided by the corresponding mean before they were combined across sessions and observers) between the first three sessions (the upper panel in Figure 5) and the last three sessions (the lower panel in Figure 5). These distributions were well fit by gamma functions,

$$f(x) = \frac{\lambda^r}{(r-1)!} x^{r-1} e^{-\lambda x}$$

(see the continuous curves shown in Figure 5), consistent with the recent report that distributions of perceptual switching rates conform to gamma functions (Brascamp et al., 2005). It is evident from Figure 5 that the long-term rivalry speeding did not appreciably alter the shape of the switching-rate distribution. The parameters of the gamma fit ($r = \lambda$ because the means have been normalized to 1) did not significantly change between the first and last three sessions (M = 5.20 [SEM = 1.17] for the first three sessions, and M = 6.33 [SEM = 1.55] for the last three sessions; $d = 0.59$, $t_6 = -1.55$, *n.s.*). Thus, while the long-term experience increased the mean rate of perceptual switches by as much as 3-fold (Figure 4), this substantial speeding occurred without measurably altering the shape of the distribution of perceptual switching rates.

We will next describe the feature-transfer results that elucidate the neural substrate of this long-term speeding in perceptual switches.

The Feature Specificity of Long-Term Rivalry Speeding

A standard stimulus and a set of feature-modified stimuli (illustrated in Figure 6A) were used to determine the feature specificity of long-term rivalry speeding. The rates of perceptual switches before and after the long-term exposure to the standard rivalry stimulus (observers attended to and reported perceptual switches during that exposure) are shown for the standard and feature-modified stimuli in Figure 6B (observers LI, MG, ES, TS, and PL). As evident from the ascending curves shown in Figure 4, perceptual switches for the standard stimulus became substantially faster following the long-term exposure (see the leftmost pair of bar graphs in Figure 6B) ($d = 4.16$, $t_4 = 9.29$, $p < 0.001$).

This speeding partially transferred to all of the feature-modified stimuli except for the hemifield-switched version (see the right side of Figure 6B). Perceptual switches became faster for the upshifted version (▲) ($d = 2.17$, $t_4 = 4.85$, $p < 0.008$), the downshifted version (▼) ($d = 1.62$, $t_4 = 3.63$, $p < 0.023$), the rotated version (Ø) ($d = 1.14$, $t_4 = 2.56$, $p < 0.063$), the eye-swapped version (◉) ($d = 1.81$, $t_4 = 4.04$, $p < 0.016$), the polarity-reversed version (Ⓟ) ($d = 1.49$, $t_4 = 3.33$, $p < 0.030$), and the components version (Ⓒ) ($d = 1.84$, $t_4 = 4.12$, $p < 0.015$), but not for the hemifield-switched version (➡) ($d = 0.59$, $t_4 = 1.33$, *n.s.*).

Although perceptual switches speeded for most of the feature-modified stimuli, the amount of their speeding was substantially reduced compared to the standard

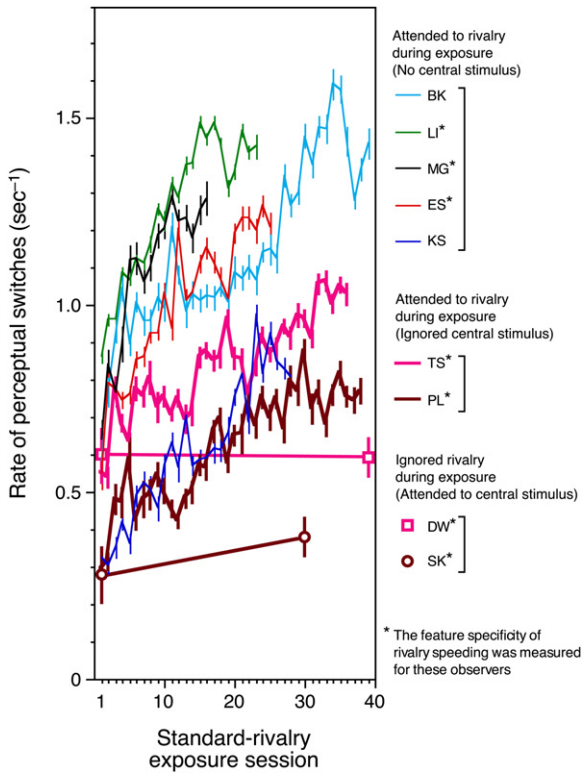

Figure 4. The Time Course of Long-Term Speeding in Binocular Rivalry

Observers BK, LI, MG, ES, KS, TS, and PL attended to binocular rivalry and reported perceptual switches during the exposure sessions. Observers DW and SK ignored binocular rivalry and reported central color changes during the exposure sessions; thus, only the pre- and post-exposure rates of perceptual switches are shown for these observers. Observers TS and PL attended to binocular rivalry while ignoring the central color changes, providing a control for the presentation of central color changes. Note that TS was matched to DW and PL was matched to SK for their initial rates of perceptual switches. It is clear from comparing TS's data with DW's and PL's with SK's that attending to binocular rivalry is necessary to induce long-term speeding in perceptual switches. The error bars indicate ±1 SEM (with trials as the random effect).

stimulus in most cases, indicating feature specificity. To evaluate the degree of feature specificity of long-term rivalry speeding, we computed the percentage by which rivalry speeding transferred to each of the feature-modified stimuli,

$$\%\text{Transfer} = \frac{\text{Speeding of switching rate for a feature-modified stimulus}}{\text{Speeding of switching rate for the standard stimulus}} \times 100\%.$$

Higher percentages indicate a greater degree of transfer of speeding, with 0% indicating no transfer at all and 100% indicating complete transfer (i.e., a feature-modified stimulus speeding as much as the standard stimulus). A percent transfer that is significantly less than 100% would indicate feature specificity, with lower percentages

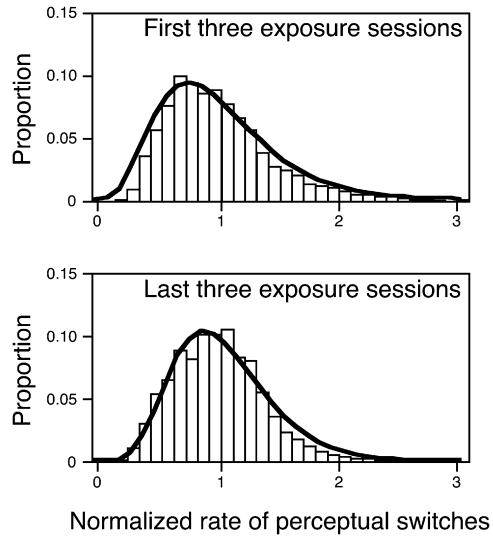

Figure 5. Normalized Distributions of Perceptual Switching Rates for the First Three Exposure Sessions (Upper Panel) and the Last Three Exposure Sessions (Lower Panel)

The continuous curves show gamma-function fits.

indicating greater degrees of feature specificity and 0% indicating complete specificity.

As shown in Figure 6C, the rivalry speeding exhibited specificity for all tested features except for the components. The percent transfer was significantly less than 100% for the upshifted version (▲) (d = 2.63, t_4 = 5.88, $p < 0.005$), the downshifted version (▼) (d = 2.17, t_4 = 4.84, $p < 0.009$), the rotated version (Ø) (d = 1.51, t_4 = 3.38, $p < 0.028$), the eye-swapped version (◉) (d = 2.89, t_4 = 6.46, $p < 0.003$), the polarity-reversed version (Ⓟ) (d = 4.51, t_4 = 10.08, $p < 0.0006$), and for the hemifield-switched version (➡) (d = 5.23, t_4 = 11.70, $p < 0.0004$). The long-term rivalry speeding was thus significantly specific for fine-scale position, fine-scale orientation, eye of origin, contrast polarity, and visual hemifield.

The percent transfer was not significantly less than 100% for the component version (Ⓒ) (d = 0.94, t_4 = 2.09, *n.s.*). However, the baseline rivalry rate for the component version was somewhat higher than that for the standard stimulus (Figure 6B). Because there is no guarantee that the rate scale is linear across different baseline rates, this nonsignificant statistical result does not necessarily suggest that the rivalry speeding fully transferred to components. We thus conclude only that the speeding substantially transferred to components.

In the Introduction, we categorized the manipulated features into low-level features (fine-scale position, fine-scale orientation, and eye of origin), which are presumably primarily coded in low-level visual areas, and multilevel features (contrast polarity and visual hemifield), which are presumably coded in multiple visual areas in the ventral stream. An inspection of Figure 6C suggests that rivalry speeding transferred less to multilevel features (see Ⓟ

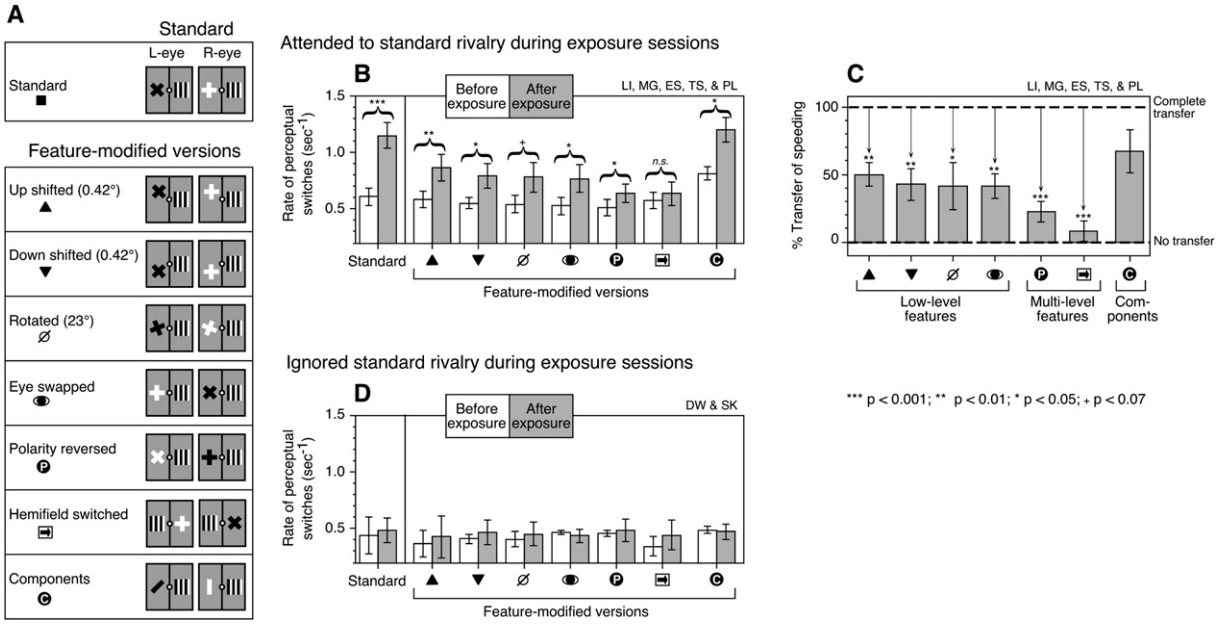

Figure 6. Feature Specificity of Long-Term Rivalry Speeding

(A) The standard stimulus (used in the long-term exposure sessions) and its feature-modified versions used to test the feature specificity of long-term rivalry speeding. In this example, the standard stimulus consists of a black "x" presented to the left eye and a white "+" presented to the right eye (at the corresponding retinal locations) in the left visual hemifield. The feature-modified versions were constructed in reference to the standard stimulus (see text for details).

(B) Perceptual switching rates before (open bars) and after (filled bars) the long-term exposure to the standard rivalry stimulus for observers who attended to and reported binocular rivalry during the exposure sessions. Significant speeding occurred for all stimuli except for the "hemifield-switched" version.

(C) The degree to which long-term rivalry speeding transferred to the feature-modified stimuli in terms of percent transfer (the speeding of feature-modified stimuli normalized to the speeding of the standard stimulus). Percent transfer was significantly less than 100% (indicating specificity) for all feature-modified stimuli except for the components version.

(D) Perceptual switching rates before and after the long-term exposure to the standard rivalry stimulus for observers who ignored binocular rivalry during the exposure sessions. As expected from Figure 4, the long-term exposure had little effect when rivalry was ignored.

For (B) and (C), the data were averaged across observers LI, MG, ES, TS, and PL. For (D), the data were averaged across observers DW and SK. The error bars indicate ± 1SEM (with observers as the random effect).

and ➡ in Figure 6C) than to low-level features (see ▲, ▼, Ø, and ◉ in Figure 6C). Indeed, the mean percent transfer of rivalry speeding was significantly less for the multilevel features (15% [SEM = 4.8%]) than for the low-level features (44% [SEM = 11%]) ($d = 1.52$, $t_4 = 3.39$, $p < 0.028$). Rivalry speeding was thus more specific for multilevel features than for low-level features.

We will next describe the results addressing the potential behavioral relevance of long-term rivalry speeding.

The Attention Dependence of Long-Term Rivalry Speeding

If long-term rivalry speeding requires attention to the rivaling stimuli, such a result would suggest that the underlying visual plasticity is engaged only when the stimuli are behaviorally relevant and gain access to awareness. We thus determined whether long-term rivalry speeding still occurred when observers ignored the rivalry stimulus. To divert attention from the rivalry stimulus, observers DW and SK were asked to continuously monitor a concurrent rapid-serial visual stream occurring at the fixation marker. The white part of a bull's-eye fixation marker rapidly changed its color, and DW and SK pulled a joystick trigger-switch whenever the color became blue or yellow. The speed of the color stream was adjusted so that this central task was attention demanding (see Experimental Procedures).

To control for the potential effect of the color-changing fixation point, we recruited observers TS and PL whose initial rates of perceptual switches were matched to DW and SK, respectively (see Figure 4). These four observers viewed exactly the same stimuli, except that DW and SK attended to the central color changes (ignoring binocular rivalry) whereas TS and PL attended to and reported binocular rivalry (ignoring the color changes). As is evident from Figure 4, rivalry speeding either did not occur at all (DW) or was minimal (SK) when the rivalry stimulus was ignored, whereas substantial speeding occurred when the rivalry stimulus was attended (TS and PL). Figure 6D confirms that the rate of perceptual switches did not change for any of the stimulus versions when binocular rivalry was ignored during the long-term exposure.

Long-term rivalry speeding thus requires that the rivaling images be attended.

DISCUSSION

We systematically investigated the time course, underlying neural substrate, and attention dependence of plasticity in the dynamics of perceptual switches in binocular rivalry. For people who experienced binocular rivalry for the first time, initially slow perceptual switches rapidly speeded (within 1–2 min of experience) to a relatively stable rate (see Figure 2). Following this initial period of instability, plasticity in the dynamics of binocular rivalry exhibited three characteristics. Rivalry slowed during each 20 s trial of continuous viewing, likely due to accumulating contrast adaptation—*short-term slowing* (confirming Lehky, 1995). When ~3 min rest intervals were given between trials for recovery from contrast adaptation (Albrecht et al., 1984), the average rate of binocular rivalry remained stable within a session of 20 repeated trials lasting about an hour—*medium-term stability* (confirming van Ee, 2005). When these sessions were repeated with intervals averaging 1.7 days, binocular rivalry speeded up to 3-fold over 14–40 sessions—*long-term speeding*.

We elucidated the neural loci of the plasticity underlying this long-term rivalry speeding by examining its feature specificity. Notably, the speeding did not transfer across visual hemifield even though the stimulus displacement was only 1.3°. This strong spatial specificity rules out contributions from nonsensory factors such as increased instability in eye fixation (van Dam and van Ee, 2006), increased arousal (e.g., caffeine speeds binocular rivalry by ~15%, George, 1936), increased voluntary attention (e.g., divided attention slows binocular rivalry by ~20%, Paffen et al., 2007), and an increased intentional effort to speed perceptual switches (e.g., intentional effort can speed binocular rivalry by more than 50% in a stimulus nonspecific manner, Lack, 1974, 1978; Meng and Tong, 2004; van Ee et al., 2005). Partial but significant specificity for eye of origin (a consciously unavailable feature) further indicates that a substantial portion of long-term rivalry speeding cannot be due to any consciously mediated strategy. Overall, the robust specificity obtained for a variety of image features (Figure 6C) indicates that neural plasticity in visual processing plays a crucial role in long-term rivalry speeding.

To implicate plasticity in low-level visual processing, long-term rivalry speeding was partially but significantly specific for image features that are coded primarily in low-level visual areas (fine-scale position, fine-scale orientation, and eye of origin). The substantial transfer of long-term rivalry speeding to the component parts is also consistent with an involvement of low-level plasticity because the experienced standard stimulus and the component stimulus were very similar with respect to their local oriented edges (coded in low-level processing) but were very different with respect to their global shapes (coded in high-level processing); the speeding therefore should not have transferred to component parts if rivalry speeding was exclusively mediated by plasticity in high-level processing. Converging evidence thus suggests that long-term rivalry speeding is at least partly mediated by neural plasticity occurring in low-level visual areas. This low-level plasticity could potentially involve changes in the response properties of low-level neurons themselves, modifications of their efferent synaptic connections, or both.

The fact that long-term rivalry speeding was not completely specific for low-level features does not necessarily implicate additional contributions from high-level plasticity. For example, it is possible that all of the underlying plasticity occurs in low-level processing and that the partial transfer is due to variability in the neural tuning within low-level visual areas. For example, orientation tuning and the degree of eye preference vary broadly from neuron to neuron in V1, even at the small retinal eccentricity we tested (e.g., Schiller et al., 1976a). The partial transfer of rivalry speeding to the rotated and eye-swapped stimuli could thus be due to the subsets of neurons in V1 with broad orientation tuning and weak eye preference, respectively. Our position shifts of 0.42°, however, were large compared to the neural receptive fields in V1 (which average less than 0.3° and under 0.4° for most neurons at an eccentricity of 0.65°; Hubel and Wiesel, 1974; Schiller et al., 1976b; Dow et al., 1981). Thus, if long-term rivalry speeding was completely mediated by neural plasticity in V1, the speeding should not have substantially transferred across 0.42° of stimulus displacement (assuming that V1 receptive fields in humans are similar to those in monkeys; Yoshor et al., 2006). It is unlikely that this partial transfer occurred due to instability in eye fixation, because the standard deviation of fixation fluctuation is known to be relatively small (ranging 0.03°–0.10°; Steinman et al., 1973; Putnam et al., 2005). Long-term rivalry speeding is thus likely to involve additional neural plasticity occurring in higher visual areas where neurons have larger receptive fields.

The strong specificity obtained for contrast polarity also suggests that V1 plasticity alone is unlikely to mediate long-term rivalry speeding. As discussed above, the 0.42° position shifts we used should be resolvable by nearly all V1 neurons at the relevant eccentricity. In contrast, the coding of contrast polarity in V1 is weak, as the polarity-selective simple cells and polarity-invariant complex cells are about equally prevalent in V1 (e.g., Schiller et al., 1976a; De Valois et al., 1982). Thus, if long-term rivalry speeding was completely mediated by neural plasticity in V1, the speeding should have transferred more to the polarity-reversed stimulus than to the 0.42°-shifted stimuli. We found the opposite. The speeding transferred significantly less to the polarity-reversed stimulus (23% transfer [SEM = 7.7%]) than to the 0.42°-shifted stimuli (46% transfer [SEM = 10%], averaged across the up and down shifts) ($d = 1.40$, $t_4 = 3.13$, $p < 0.036$). This implicates contributions from high-level visual neurons, as many of them exhibit selectivity for contrast polarity (e.g.,

Desimone and Schein, 1987; Levitt et al., 1994; George et al., 1999), with 60% of anterior IT neurons reducing their responses by more than 50% when their preferred stimuli were contrast-reversed (Ito et al., 1994).

The overall pattern of visual-feature specificity, characterized by (1) the complete (or nearly complete) specificity for features coded in both low- and high-level ventral visual areas (visual hemifield and contrast polarity), (2) the moderate but significant specificity for features primarily coded in low-level visual areas (fine-scale position, fine-scale orientation, and eye of origin), and (3) the strong transfer to component parts, is consistent with the hypothesis that the long-term speeding of perceptual switches in binocular rivalry involves neural plasticity (changes in neural responses, modifications of efferent synaptic connections, or both) occurring in both low- and high-level visual areas in the ventral stream. This result is consistent with the current view that the mutually exclusive perceptual switches observed during binocular rivalry are the net result of inhibitory interactions occurring in multiple visual areas (e.g., Blake and Logothetis, 2002; Suzuki and Grabowecky, 2002a, 2002b; Wilson, 2003; Alais and Blake, 2005; Freeman, 2005; Pearson and Clifford, 2005; Tong et al., 2006).

The current models of binocular rivalry postulate signal transduction, adaptation, inhibitory interactions, and stochastic noise as the primary parameters that control the dynamics of perceptual switches (e.g., Laing and Chow, 2002; Wilson, 2003; Kim et al., 2006). Future research needs to determine how these factors are modified by long-term rivalry experience and how those modifications contribute to rivalry speeding. Nevertheless, the current result provides a constraint that, whatever the underlying neural mechanisms of plasticity might be, they must substantially speed perceptual switches without appreciably altering the shape of the distribution of switching rates.

Finally, the long-term speeding of perceptual switches reported here shares some basic characteristics with perceptual learning. Similar to rivalry speeding, perceptual learning often exhibits specificity for basic image features such as position, orientation, spatial frequency, size, motion direction, and eye of origin (e.g., Fiorentini and Berardi, 1980; Ball and Sekuler, 1982; Karni and Sagi, 1991, 1993; Polat and Sagi, 1994; Ahissar and Hochstein, 1996). In many instances, perceptual learning is also attention dependent in that training selectively improves processing of the attended aspects of the stimuli (e.g., Shiu and Pashler, 1992; Ahissar and Hochstein, 1993, 2000; Fahle, 1994, 2004; but see Aslin et al., 2002; Watanabe et al., 2002b).

One important difference between perceptual learning and rivalry speeding, however, is that the former is goal directed, but the latter is not. In a perceptual learning experiment, observers make an intentional effort to accurately perform the to-be-learned task. Furthermore, to improve on the task, attention needs to select the stimulus features that are task relevant, so that the neural processes that are effective for processing those task-relevant features can be fine-tuned with practice (see Ahissar and Hochstein, 2004, and Suzuki, 2005, for relevant discussions). Consistent with this idea, feature specificity of perceptual learning depends on task requirements. For example, learning is specific for low-level features only when the task requires fine-resolution discrimination of low-level features such as position and orientation (Ahissar and Hochstein, 1997, 2004). It is thus not surprising that perceptual learning often depends on attention; learning occurs when observers perform the to-be-learned task by attending to the task-relevant aspects of the stimuli, but learning does not occur when observers experience the same stimuli but perform a different task by attending to aspects of the stimuli that are not relevant to the to-be-learned task.

In contrast, long-term rivalry speeding occurs in the absence of any particular goal or any intentional effort to speed perceptual switches. During the postexperiment debriefing, none of our observers stated that they made any intentional effort to influence the dynamics of binocular rivalry. The nature of attention dependence is also different between perceptual learning and rivalry speeding. Whereas attention needs to select task-relevant features to improve task performance in perceptual learning, long-term rivalry speeding occurs when the competing stimuli are simply attended in order to be reported. It appears as if attention and/or awareness is acting like an on-off switch in the case of rivalry speeding, and this provides a clue regarding the potential behavioral relevance of long-term rivalry speeding. Because people tend to voluntarily attend to stimuli that are behaviorally relevant in real-life situations, we can at least infer that the speeding occurs only for the processing of behaviorally relevant stimuli. As for what behavioral benefits long-term rivalry speeding might confer, we can only speculate that long-term speeding in perceptual switches might reflect general mechanisms that adaptively speed assessments of alternative scene interpretations when a frequently encountered scene contains multiple behaviorally relevant interpretations.

To summarize, we systematically examined plasticity in the dynamics of perceptual switches in binocular rivalry. In addition to confirming previous reports that the rate of perceptual switches slowed over the short term (~20 s) and remained stable over the medium term (~1 hr), we demonstrated that perceptual switches substantially speeded (up to 3-fold) over the long term (months). The overall pattern of feature specificity of this long-term rivalry speeding suggested that the speeding involved neural plasticity occurring in both low- and high-level visual areas in the ventral stream. The fact that long-term rivalry speeding was switched on and off by voluntary attention suggested that the speeding selectively affects the processing of behaviorally relevant stimuli. One remaining question is whether the long-term speeding of perceptual switches in binocular rivalry reflects general mechanisms that also affect other types of perceptual switches, such as monocular rivalry (perceptual switches between translucently

overlapped images), figural rivalry (perceptual switches between two or more interpretations of the same figure), and attention shifts. Although this is an open empirical question, recent results are encouraging, as they suggest that binocular rivalry and other types of perceptual switches (e.g., Brascamp et al., 2005; Pearson and Clifford, 2005), including attention shifts (e.g., Wilson et al., 2000), share fundamentally similar mechanisms (also see Leopold and Logothetis, 1999; Blake and Logothetis, 2002, and Tong et al., 2006, for related discussions).

EXPERIMENTAL PROCEDURES

Observers

We found that perceptual switches could be initially very slow for those who experience binocular rivalry for the first time. To determine the length of this initial period of instability in binocular rivalry, 40 Northwestern University undergraduates were recruited. These students had no prior experience with binocular rivalry and received partial course credit for their participation. Nine additional participants were recruited to investigate long-term rivalry speeding. MG (an author) was a psychophysically trained observer; BK, LI, ES, KS, DW, TS, and PL were paid or unpaid student volunteers; and SK participated for partial course credit. None of these nine observers had previously participated in a binocular-rivalry experiment, but they were given a sufficient number of practice trials to eliminate the initial period of unstable and slow switches. All observers had normal or corrected-to-normal visual acuity and all gave informed consent prior to participation.

Stimuli and Procedure

The rivalry stimuli were a "standard stimulus," consisting of rivaling "+" and "x" shapes, and its feature-modified variants; these are illustrated in Figures 1 and 6. The shapes were presented against a gray immediate background (44.6 cd/m^2, CIE[.317, .322]) on a 21 inch Sony color monitor (75 Hz) in a dimly lit room, using Vision Shell software (Micro ML, Inc.). The two rivaling shapes were always opposite in contrast polarity (i.e., when + was white, x was black, and vice versa). The luminance of the white stimulus was 119 cd/m^2 (CIE[.317, .319]) and the black stimulus was 17.0 cd/m^2 (CIE[.319, .321]), yielding Michelson contrasts of about ±0.45.

A stereoscope consisting of four front-surface mirrors and a central divider was used to dichoptically present the rivaling shapes (i.e., to present one shape to each eye). A head rest was used to stabilize the viewing distance at 110 cm. To facilitate exclusive binocular rivalry (i.e., clear perceptual alternations between the rivaling shapes without perception of mixed parts from both shapes), the rivaling patterns were small (0.81° visual angle in linear extent), opposite in contrast polarity, consisted of differentially oriented edges (i.e., vertical/horizontal versus diagonal), and were presented parafoveally (~0.65° eccentricity) to the left or right of the central fixation marker. The bull's-eye-shaped central fixation marker and a high-contrast textured frame were binocularly presented to facilitate stable binocular alignment. A vertical grating was also binocularly presented in the visual hemifield opposite to the rivaling stimuli to balance the stimulus configuration and facilitate stable central fixation (see Figure 1). Because the obtained long-term rivalry speeding was completely specific to lateral position (0.65° to the left or right of the fixation marker), we are confident that our observers reliably maintained central eye fixation.

On each trial, the observer continuously viewed the rivalry display for 20 s while fixating the central bull's-eye fixation marker. Whenever the perceived shape changed, the observer indicated the newly perceptually dominant shape by pressing a corresponding joystick button (e.g., pressing the right button when the "+" shape became dominant, and pressing the left button when the "x" shape became dominant). In cases where the rivalry was not completely exclusive (i.e., when the suppressed pattern was not completely invisible), the observer was instructed to respond to the perceptually dominant shape. The duration of each perceptual dominance was computed from the time differences between successive button presses. We then reciprocally transformed the duration data into a measure of the rate of perceptual switches for analyses (see the main text).

Note that because our stimuli were small (<1°) and were parafoveally presented, the incidences of "mixed" percepts (seeing the mixture of the two shapes with no clear dominance) were infrequent (e.g., Blake et al., 1992). Nevertheless, to make sure that long-term rivalry speeding was not accompanied by systematic changes in the frequency of mixed percepts, we instructed observers TS and PL to report mixed as well as exclusive percepts on the last trial of each session; they indicated mixed percepts by simultaneously pressing both the left and right buttons, while pressing only one button for the cases of clear perceptual dominance. The overall time proportion of mixed percepts was 12% for TS (across 34 sessions) and 6% for PL (across 36 sessions), but the proportions did not significantly change over the course of the long-term rivalry sessions ($r = -0.015$, $t_{32} = -0.083$, *n.s.* for TS, and $r = -0.20$, $t_{34} = -1.19$, *n.s.* for PL).

Because each trial was automatically terminated after 20 s, the last perceptual dominance was truncated. Though it may seem appropriate to always discard the truncated last dominance duration from each trial, this was problematic when we examined the initial period of instability in rivalry-naive observers because perceptual dominance durations widely fluctuated in the first several trials. In those initial trials, simply discarding the last dominance duration would have yielded unrepresentatively short estimates of average perceptual dominance durations (note that we actually analyzed the reciprocal of perceptual dominance durations [i.e., perceptual switching rates] as described in the Results section, but here we stick with dominance durations to make the explanation more intuitive). For example, suppose that the first perceptual dominance lasted 3 s and the next dominance persisted through the end of the trial. This second dominance would have been longer than 17 s, and discarding it would yield an unreasonably short estimate of 3 s. As a compromise, we included the truncated last dominance duration only when it was longer than the average of the preceding dominance durations. The rationale was as follows. If the truncated last dominance duration was longer than the preceding average, the "true" trial average including the untruncated version of the last duration would certainly have been longer than the preceding average. Thus, including the truncated last duration would improve the average dominance duration estimate. In contrast, if the truncated duration was shorter than the preceding average, we could not know whether including or discarding the truncated duration would yield a better estimate. We thus included the truncated last dominance duration in the former case and discarded it in the latter case. The truncated last dominance durations, however, were always discarded when we analyzed how perceptual switching rates changed within each trial, because the above-mentioned inclusion algorithm could have biased the analysis toward obtaining within-trial slowing.

Examining Initial Instability

All 40 observers saw the same rivalry stimulus (a black "x" presented to the left eye and a white "+" presented to right eye in the left visual hemifield). A practice trial was given prior to the experimental trials so that observers became familiar with the task of responding to the alternating percepts of the rivaling shapes. In the practice trial, observers responded to "simulated" binocular rivalry in which the left-eye shape and the right-eye shape were physically alternated (with a blank field presented to the corresponding region in the other eye) following a typical time course of actual binocular rivalry. Sixteen of the 40 observers were then tested in ten consecutive trials (with an ~3 min break between trials). Because it became apparent that the initial slow perceptual switching rapidly speeded to a relatively stable

rate within about four trials, the remaining 24 observers were tested only in five consecutive trials (see Figure 2).

Examining Long-Term Rivalry Speeding

All observers who participated in the long-term rivalry experiments were given a sufficient number of practice trials with the standard stimulus to eliminate the initial period of rapid speeding. To determine the feature specificity of long-term rivalry speeding, we administered (1) pre-exposure sessions in which the baseline perceptual switching rates were measured for the standard and feature-modified stimuli, (2) exposure sessions in which observers repeatedly experienced binocular rivalry for the standard stimulus over many days until the rivalry speeded substantially, and (3) post-exposure sessions in which perceptual switching rates were again measured for the standard and feature-modified stimuli to evaluate transfer of long-term rivalry speeding to the feature-modified stimuli.

The standard stimulus consisted of a black "x" shape presented to the left eye and a white "+" shape presented to the right eye. The standard stimulus was presented in the left visual hemifield for observers BK, MG, KS, DW, SK, TS, and PL (as shown in Figure 6A), and in the right visual hemifield for LI and ES. Relative to the standard stimulus, the shapes were shifted up and down by 0.42° (while preserving retinal eccentricity at 0.65°) in the upshifted and downshifted versions, the shapes were each rotated clockwise by 23° in the rotated version, the shape-to-eye assignment was swapped in the eye-swapped version, and the contrast polarity was reversed for each shape in the polarity-reversed version. All of these feature-modified versions were also tested in the opposite visual hemifield for LI, MG, and ES. Because long-term rivalry speeding did not transfer across visual hemifield, we averaged the data across these hemifield-switched versions. For DW, SK, TS, and PL, only the standard stimulus was tested in the opposite visual hemifield. Finally, the components version consisted of the vertical part from the "+" shape rivaling with the rightward-slanted part from the "x" shape. The transfer effects were not measured for BK and KS.

In each pre-exposure session, all stimulus versions were tested once (with an ~3 min break between trials). The standard stimulus was tested twice (in the first and last trials) for some of the observers (LI, MG, and ES) to confirm that the rivalry for the standard stimulus remained stable within a session. One or two sessions were given per day, and the data were averaged across the pre-exposure sessions (four sessions for LI, MG, and ES, and six sessions for DW, SK, TS, and PL) to establish the baseline perceptual switching rate for each stimulus version. The post-exposure data were obtained in the same way. The pre-exposure and post-exposure rates of perceptual switching were compared for each stimulus version to assess the feature specificity of long-term rivalry speeding. Trials were given in the same order in the pre-exposure and post-exposure sessions, so that any possible sequential effects would be equivalent in those sessions and thus could not account for the obtained pattern of feature specificity.

Each exposure session consisted of 20 consecutive trials (with an ~3 min break between trials) of experiencing binocular rivalry with the standard stimulus. All observers except LI were given exposure sessions with intervals greater than 12 hr. The average intersession intervals were 1.7 days for BK, 0.6 days for LI, 2.6 days for MG, 2.5 days for ES, 1.1 days for KS, 1.4 days for DW, 1.2 days for SK, 1.9 days for TS, and 1.6 days for PL. For the observers who attended to and reported binocular rivalry (BK, LI, MG, ES, KS, TS, and PL), the exposure sessions continued until the rivalry substantially speeded and the speeding curve (as a function of session) reached an apparent asymptote.

To test the role of attention, comparable numbers of exposure sessions were given to DW and SK who ignored binocular rivalry during exposure (see Figure 4). They were repeatedly exposed to binocular rivalry for the standard stimulus as described above, but they attended to a central task and ignored the rivaling patterns. The white part of the bull's-eye fixation marker (see Figure 1) changed color every 536 ms among six colors: red (21.9 cd/m^2, CIE[.619, .345]), green (34.8 cd/m^2, CIE[.309, .581]), purple (26.8 cd/m^2, CIE[.244, .136]), gray (29.9 cd/m^2, CIE[.317, .323]), blue (28.9 cd/m^2, CIE[.196, .152]), and yellow (73.9 cd/m^2, CIE[.438, .489]). Observers attended to these central color changes and pulled the joystick trigger whenever the color became either blue or yellow. The fact that both observers yielded superior but unsaturated performance on the central task indicated that attention was sufficiently engaged by the central task; the average error rates were 0.046 and 0.040, respectively, for DW and SK, and these values were obtained by computing |[# of targets] – [# of trigger clicks]|/[# of targets] for each trial and averaging the values across all trials.

To control for the presence of the color-changing fixation point, observers TS and PL viewed the same displays as did DW and SK, except that TS and PL attended to and reported binocular rivalry and ignored the color changes in the fixation bull's-eye. Furthermore, the initial rate of perceptual switching was matched for DW and TS and for SK and PL (see Figure 4).

ACKNOWLEDGMENTS

This work was supported by National Institutes of Health grant EY14110 and National Science Foundation grant BCS0643191.

Received: July 18, 2006
Revised: June 10, 2007
Accepted: September 19, 2007
Published: November 20, 2007

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