



## Rival ideas about binocular rivalry

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### Abstract

Binocular rivalry has been used to investigate neural correlates of visual awareness. For this investigation to succeed, however, it is necessary to know what rivals during binocular rivalry. Recent work has raised questions about whether rivalry is between eyes or between stimuli. We find that stimulus rivalry occurs only within a limited range of spatial and temporal parameters—otherwise eye rivalry dominates. © 1999 Elsevier Science Ltd. All rights reserved.

*Keywords:* Binocular rivalry; Spatial frequency; Temporal frequency

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Techniques in neuroscience have evolved to the point where it is feasible to study the neural concomitants of conscious awareness, a problem of long-standing interest in philosophy, psychology and brain science (Crick, 1994). One particularly promising strategy for tackling this question exploits a well-known bistable phenomenon—binocular rivalry—as a means for dissociating physical stimulation and conscious visual experience (Logothetis & Schall, 1989; Leopold & Logothetis, 1996; Lumer, Friston & Rees, 1998).

A classic configuration for producing binocular rivalry entails dichoptic presentation of two orthogonal gratings. When those gratings are relatively small in angular subtense, observers usually see one pattern or the other for several seconds, with dominance fluctuating unpredictably over time (Fox & Herrmann, 1967). But what dominates in this situation, a particular stimulus or the region of the eye upon which the dominant stimulus is imaged? If binocular rivalry is to provide an understanding of how conscious awareness is implemented by the brain, it is essential to get the answer to this question right.

Several lines of psychophysical evidence implicate eye dominance, not stimulus dominance. Consider the eye swapping procedure. Observers depress a switch when the rival pattern shown to one eye is dominant in its

entirety, the other being completely suppressed from vision. If this keypress causes the immediate interchange of the left- and right-eye patterns, the previously dominant pattern will now be shown to the previously suppressed eye and vice versa. When this happens, the outcome is clear (Blake, Westendorf & Overton, 1979): the dominant pattern abruptly becomes invisible and the previously suppressed pattern becomes dominant—it is an eye that dominates, not a particular stimulus. Next, consider the stimulus change procedure. Here the orientation, the spatial frequency or the direction of motion of a stimulus is changed while that stimulus is suppressed. These changes, regardless how large, go unnoticed until seconds later when the suppressed eye returns to dominance—again, it is an eye that is suppressed, not a particular pattern (Blake & Fox, 1974; Blake, Yu, Fukuda & Lokey, 1998).

This view was recently challenged by Logothetis, Leopold and Sheinberg, (1996) who reported novel stimulus conditions that purportedly refute the ‘eye’ interpretation of binocular rivalry. Using a variant of the eye interchange technique, they repetitively exchanged the two eyes patterns every 333 ms. In addition, both rival targets (orthogonally oriented gratings) were rapidly flickered at 18 Hz. Viewing relatively low contrast gratings, their observers reported fluctuations in visibility between the rival targets, following a slow, irregular time-course resembling conventional rivalry. Logothetis et al. dubbed this ‘stimulus rivalry’ as the extended durations of exclusive dominance were longer

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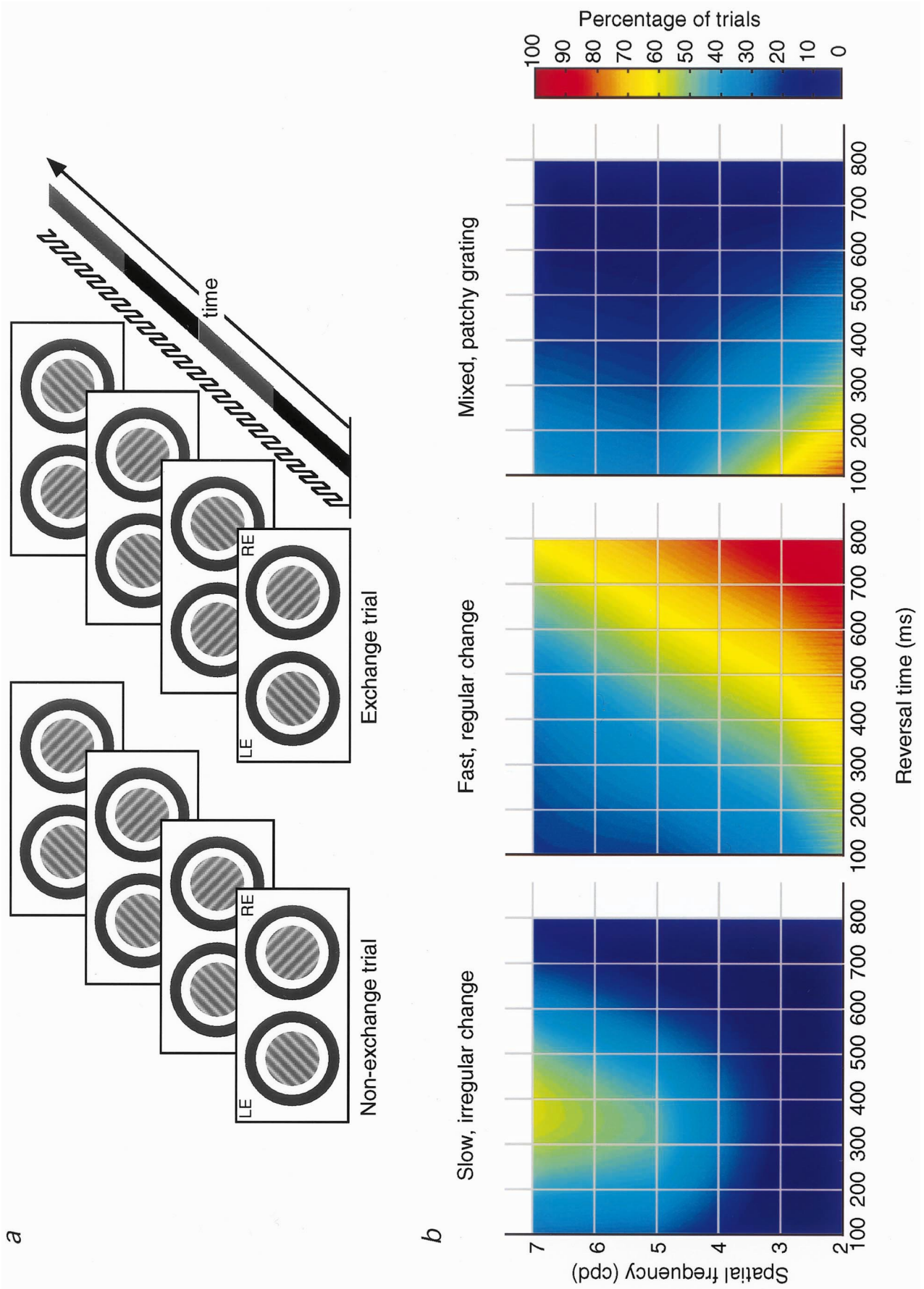


Fig. 1. (Caption opposite)

than the exchange rate. Generalizing from their results, Logothetis et al. concluded that rivalry under conventional conditions, wherein stimuli are not swapped between the eyes, also entails alternations in dominance between competing stimuli, not between competing eyes.

Intrigued by their observations but puzzled by the generality of their conclusion, we have performed additional experiments comparing ‘eye’ versus ‘stimulus’ rivalry. Our results demonstrate that ‘stimulus rivalry’—unlike conventional binocular rivalry—only occurs under very limited conditions which, in fact, correspond to those known to disrupt conventional binocular rivalry.

## 1. Methods

Rival displays were generated by a Power PC computer running at 225 MHz using Matlab in conjunction with the Psychophysics Toolbox (Brainard, 1997) and were displayed on the two halves of a 21' NEC Multi-Synch E1100 video monitor (1024H × 768V pixel resolution; 72 frames s<sup>-1</sup>) located 100 cm from the eyes of the observer. Stimuli were circular patches (1.7° in diameter) of sinusoidal gratings, with orthogonal orientations presented to the two eyes. Observers viewed these rival grating targets by way of a mirror stereoscope. Left- and right-eye gratings were surrounded by dark circular rings 2.0° in diameter, providing strong fusion contours that promoted stable binocular alignment. Except where noted, grating contrast was 25%, spatial frequency was 3, 5 or 7 c deg<sup>-1</sup> in Experiment 1 and 7 c deg<sup>-1</sup> in Experiment 2. Space average luminance of the gratings always was 21 c deg<sup>-1</sup> m<sup>-2</sup>, and the luminance of the background was 1.5 c deg<sup>-1</sup> m<sup>-2</sup>. On each trial observers viewed a given pair of rival gratings for 10 s. For each condition, 50 such trials were administered, with all conditions randomly intermixed during a testing session.

## 2. On the generality of ‘stimulus’ rivalry

Conventional binocular rivalry occurs over a wide

range of conditions involving dissimilar stimulation of the two eyes (Fox, 1991). However, Logothetis et al. (1996) reported ‘stimulus’ rivalry for only a narrow range of specific stimulus conditions. If ‘stimulus’ rivalry is synonymous with binocular rivalry, it should occur over the same wide range of stimulus conditions associated with conventional rivalry, and that was the purpose of our first experiment. In addition, we were concerned about the methodology employed by Logothetis et al. (1996). Their observers were asked to track fluctuations in dominance between two rival stimuli by pressing one of two keys during a 2 min viewing period during which rival patterns were exchanged between the eyes at 3 Hz. But if observers were to experience ‘eye’ rivalry, they could not have responded accurately, since dominance would have repetitively switched between stimuli three times per second, a rate too rapid to track reliably by button presses.

In view of this methodological concern, we employed an alternative reporting technique not biased against eye rivalry. After viewing a given display for 10 s, observers indicated which of three response categories best described what they saw: (i) ‘slow, irregular change’, (ii) ‘rapid, regular change’ and (iii) ‘mixed and patchy’. The first category corresponds to the percepts predicted by ‘stimulus rivalry’ (slow, irregular changes in the dominant orientation). The second category corresponds to ‘eye rivalry’ (rapid, regular change between the two orientations). The third category indicates incomplete rivalry and/or binocular superimposition. On some trials, rival stimuli were exchanged between the eyes, following the procedure of Logothetis et al. (1996), and on other trials the two rival targets were presented to the same eyes throughout the 10 s viewing period. Observers did not manually track fluctuations in rivalry during this viewing period, and they had no trouble performing the categorization task.

We tested four observers with normal binocular vision, including three of whom were naive about the purpose of the experiments. On non-exchange trials (conventional display, Fig. 1a), a leftward tilted (−45°) grating was shown to one eye and a rightward tilted

Fig. 1. Schematic diagram of stimulus display. (a) Time course of a non-reversal trial and a reversal trial. (b) Results from Experiment 1, showing average results for four observers (all of whom gave comparable results). Color signifies the percentage of trials on which a given response category was employed as a function of spatial and temporal frequency. The left-hand diagram gives the percentage of trials on which observers reported ‘slow, irregular change’, the middle panel the incidence of ‘fast, irregular change’, and the right-hand panel the incidence of ‘patchy/superimposed gratings’. Not shown are data for the non-swapping condition—observers reported ‘slow, irregular’ change on 99% of these trials. These plots were produced in the following way. For each spatial frequency tested, the actual data (the percentage of a given category report as a function of reversal time) were fitted by a function giving the smallest least-squared error (which always yielded  $r^2$  values in excess of 0.95). Percentage values between the sampled spatial frequencies were then interpolated from that function and color-coded as shown in these graphs. Actual data for individual observers in this and the next experiment (Fig. 3) may be accessed by navigating on the WWW to: <http://www.psy.vanderbilt.edu/faculty/blake/Rivalry/leeblake1.html>.

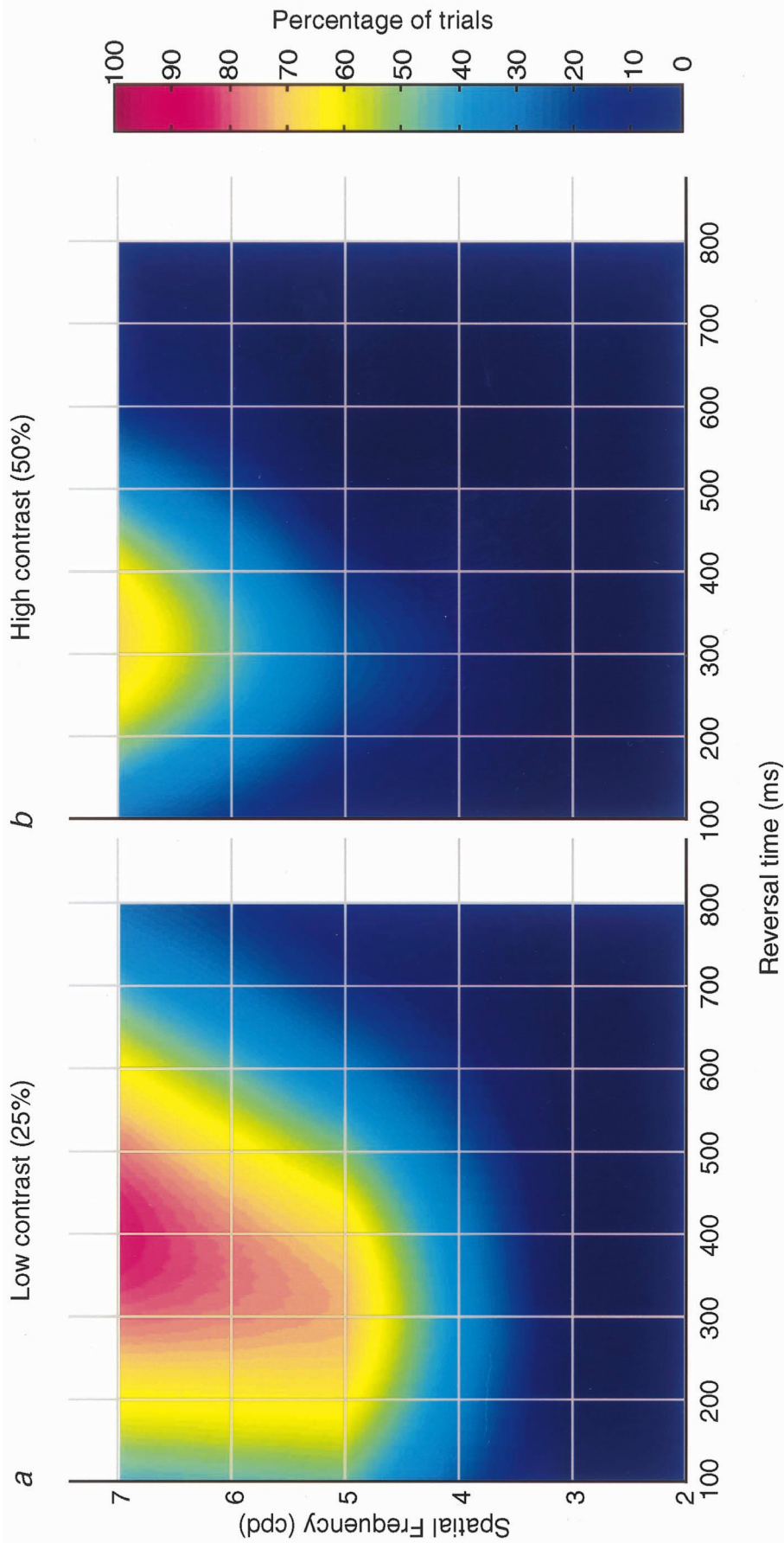


Fig. 2. Results from a replication of Experiment 1 comparing the incidence of 'stimulus' rivalry with low contrast (25%) and high contrast (50%) gratings. Three observers were tested, two who participated in Experiment 1 and a third individual new to the task. In all other respects, this replication was identical to Experiment 1. The two figures plot the incidence of 'slow, irregular change' (i.e. 'stimulus' rivalry) for eye-exchange conditions measured with low and high contrast gratings. Not shown are data for the non-exchange conditions; on those trials observers experienced conventional rivalry on essentially all trials, as expected.



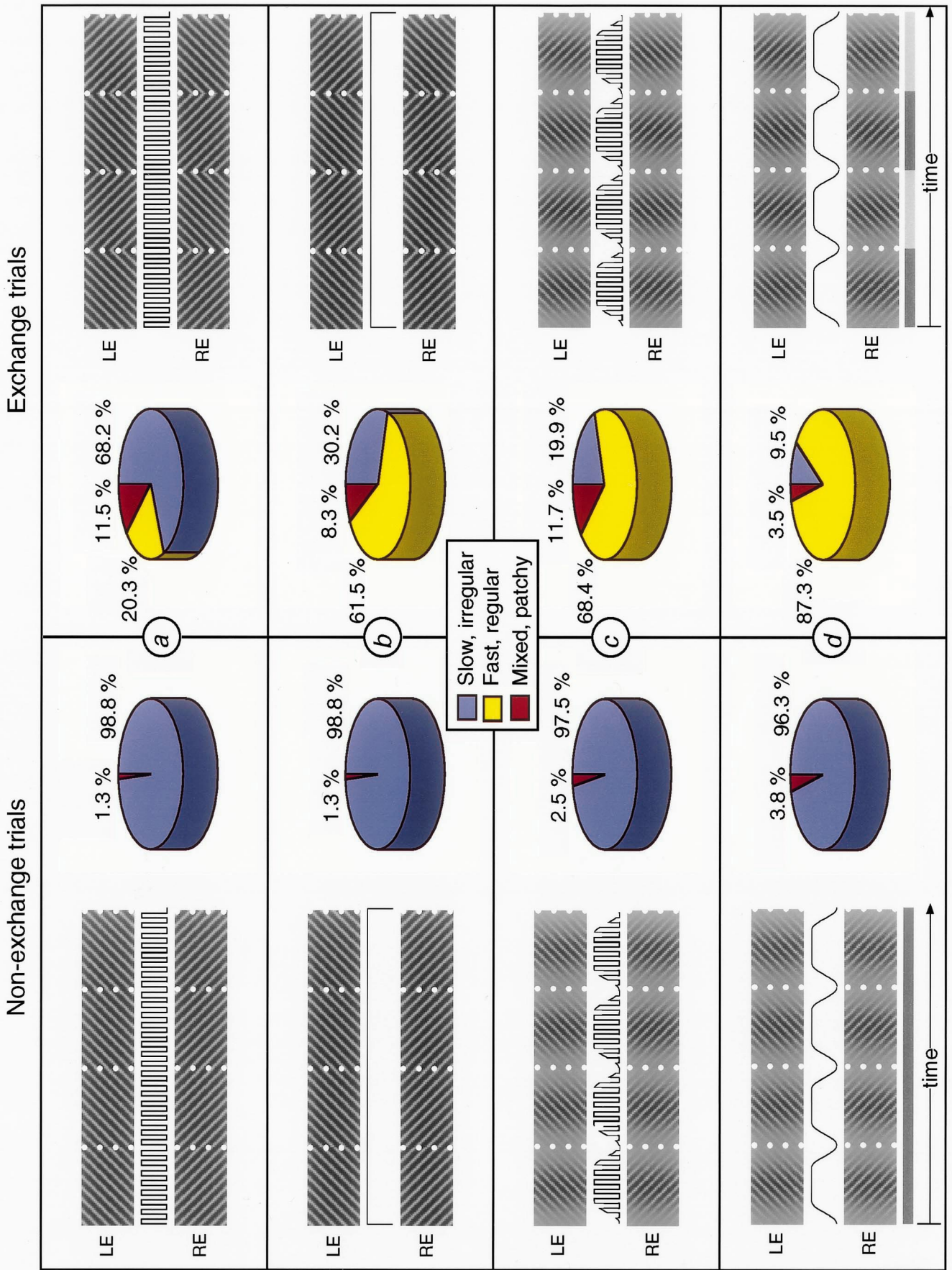


Fig. 3. (Caption overleaf)

(45°) grating was shown to the other eye for the entire duration of the 10 s trial. On exchange trials, the two gratings were swapped between the two eyes regularly as indicated schematically by the light/dark stripe in Fig. 1a, with the reversal rate ranging from 1.4 Hz (722 ms exposure duration/swap) to 6 Hz (167 ms/swap). In addition, the gratings also flickered on and off at 18 Hz throughout the trial as indicated schematically by the square-wave sequence over time in Fig. 1a, replicating the conditions employed by Logothetis et al. For both types of trials (non-exchange and exchange) rival gratings were always identical in spatial frequency, either 3, 5 or 7 c deg<sup>-1</sup>, and identical in contrast (25%). In addition, ‘catch trials’ were randomly intermixed with the other trials to insure that observers understood the task and were performing honestly. On these catch trials, a grating was presented to one eye but not to the other, and that grating either changed in orientation slowly every couple of seconds (resembling ‘slow, irregular change’) or rapidly several times a second (resembling ‘rapid, regular change’). Performance on these catch trials confirmed that observers were following instructions.

Observers should experience relatively slow, irregular alternations in dominance on the non-reversal trials, for these trials simply constitute a conventional binocular rivalry situation. Consistent with this expectation, the incidence of ‘slow, irregular change’ was almost 100% for all four observers, regardless of grating spatial frequency. Moreover, if these slow changes in dominance are, in fact, ‘stimulus’—not ‘eye’—rivalry, we also expect a high incidence of ‘slow, irregular’ reports in the exchange conditions where the two rival patterns were swapped repetitively between the eyes. Contrary to prediction, however, ‘slow, irregular’ change occurred only under very restricted conditions that were consistent across observers (Fig. 1b). With eye-swapping, observers primarily saw rapid, regular change (evidence for ‘eye’ rivalry) except when reversal rate was rapid and grating contrast was low, in which case observers tended to experience binocular mixtures in which one grating appeared superimposed on the other (Fig. 1c). We repeated this entire set of measurements

using gratings of 50% contrast. Now the incidence of ‘stimulus’ rivalry was even further reduced, with the overwhelming majority of trials eliciting reports of ‘fast, regular change’ indicative of ‘eye’ dominance (Fig. 2). Under conventional, non-exchange conditions, observers invariably reported ‘slow, irregular change’ indicative of normal binocular rivalry<sup>2</sup>.

### 3. Role of transients in ‘stimulus’ rivalry

Thus with the eye-swapping procedure, the conditions yielding ‘stimulus’ rivalry are quite restricted and much narrower than those yielding conventional rivalry. But what accounts for the incidence of ‘stimulus’ rivalry under these restricted conditions? Results from a second experiment indicate that the temporal conditions employed by Logothetis et al. provide the key.

It is well known that dominance of one rival target is easily broken by introducing abrupt transients in the other, suppressed target (Walker & Powell, 1979; Blake, Westendorf & Fox, 1990). For example, simply turning a rival target briefly off and back on again can prematurely switch dominance. Logothetis et al. flickered both rival targets at 18 Hz and swapped those targets abruptly back and forth between the eyes at 3 Hz. Their targets, in other words, produced a steady train of abrupt transients in both eyes. Are flicker and abrupt transients important ingredients for producing ‘stimulus’ rivalry under those limited conditions where it is observed? To find out, we selected contrast, spatial frequency and reversal rate values yielding a relatively high incidence of ‘stimulus’ rivalry in our Experiment 1. We then remeasured the incidence of ‘slow, irregular change’ and ‘rapid, regular change’ under four eye-

<sup>2</sup> The values of spatial frequencies and grating size used in our experiment were selected to maximize the incidence of unambiguous rivalry under nonswapping conditions. We have not examined stimulus versus eye rivalry over the entire range of visible spatial frequencies, so the ‘maps’ in Fig. 1 remain incomplete. And from other work (O’Shea, Sims & Govan, 1997) we know that spatial frequency effects in rivalry vary with grating size, so the particulars of these maps might also change with stimulus size.

Fig. 3. Role of transients in production of ‘stimulus’ rivalry. On exchange trials, gratings were swapped between the eyes every 444 ms while on non-exchange trials gratings were not exchanged. (a) Abrupt grating change with rapid flicker. (‘abrupt’ meaning that the change occurred during a single video retrace). (b) Abrupt change and no flicker. (c) Gradual change with rapid flicker. Gratings flickering rapidly at 18 Hz were introduced and removed gradually over time, with the rise time and fall time corresponding to ten video frames (139 ms). (d) Gradual change and no flicker. This condition was the same as the condition (c) except that gratings were not flickering. The four conditions in non-reversal trials were different from their corresponding conditions in reversal trials only in that the orientation of gratings remained unchanged in each eye during the entire duration of the 10 s trial. Thus on ‘abrupt’ change trials the gratings, in fact, appeared continuous, and on the ‘gradual’ change trials the gratings appeared to fade on and off repetitively throughout the 10 s observation period. Results from Experiment 2 are summarized in the pie-charts, with each chart showing the percentage of trials on which observers reported each of the three response categories for each of the four conditions of flicker/swapping. We performed a 2 × 2 × 2 ANOVA on the ‘slow, irregular’ responses, with trial type (exchange vs. non-exchange), flicker mode (flicker vs. no-flicker) and abruptness (abrupt vs. gradual) as variables. All three variables produced significant main effects ( $P < 0.05$ ); also statistically significant were the interactions between trial type and flicker mode ( $F(1, 3) = 10.9, P < 0.05$ ), trial type and abruptness ( $F(1, 3) = 16.1, P < 0.05$ ), and trial type, flicker mode and abruptness ( $F(1, 3) = 34.9, P < 0.01$ ).

swapping conditions: (1) rival gratings were swapped abruptly between the eyes and were flickered on and off at 18 Hz; (2) gratings were swapped abruptly but were not flickered; (3) gratings were swapped gradually and were flickered; and (4) gratings were swapped gradually but were not flickered. For purposes of comparison, we also tested the same four conditions except that rival gratings were not exchanged between eyes (Fig. 3).

On non-exchange trials, observers experienced 'slow, irregular' changes between the two gratings whether or not they were flickered or were turned on and off gradually—these reports correspond to conventional binocular rivalry (Fig. 3). However, on eye-swap trials (Fig. 3) 'slow, irregular' change (i.e. 'stimulus' rivalry) only occurred when flickering gratings were abruptly exchanged between the eyes. The incidence of 'stimulus' rivalry decreased dramatically when rival gratings were gradually exchanged between the eyes or when they were stationary, not flickering. The combination of stationary gratings and gradual exchange essentially abolished 'stimulus' rivalry. This differential effect of transients on the 'slow, irregular' changes during non-exchange and during exchange trials was evident in each observers data and was substantiated by results from analysis of variance (see caption to Fig. 3). Based on these results, we conclude that the swapping paradigm devised by Logothetis et al. disrupts normal binocular rivalry by virtue of the repeated transients associated with the eye exchange procedure. Moreover, we would expect any stimulus manipulation involving rapid, repetitive, abrupt transients to disrupt binocular rivalry, including color swapping like that employed by Logothetis et al.

#### 4. Conclusion

We have identified stimulus conditions which, when viewed without eyeswapping, yield the slow, irregular changes in dominance characteristic of conventional binocular rivalry. However, these same stimulus conditions, when viewed during rapid swapping of patterns between eyes, predominately yield rapid, regular changes in dominance or mixed dominance. With the Logothetis et al. eyeswapping procedure, 'stimulus' rivalry is seen primarily with relatively low contrast patterns within a rather narrow range of spatial and temporal frequencies, and then only when those patterns are flickered rapidly and exchanged abruptly between the eyes. These limited conditions may be what Logothetis et al. were referring to when they wrote that "the effect reported here appears to vary in strength as the contrast or the type of stimulus changes" (p. 624). It is noteworthy that these same stimulus conditions can disrupt (Walker & Powell, 1979; Wolfe, 1983; Liu, Tyler & Schor, 1992; Yang, Rose & Blake, 1992) or

retard (O'Shea & Crassini, 1984) binocular rivalry under conventional viewing without eye-swapping.

To reiterate our finding, the conditions yielding 'stimulus' rivalry are narrower than those yielding conventional rivalry. Thus 'stimulus' rivalry and 'eye' rivalry are distinct and, therefore, arise from different mechanisms. It was an overstatement to conclude that "it is the 'stimulus' and not the 'eye' that competes for dominance during rivalry" (p. 624 Logothetis et al., 1996). However, limiting the scope of the results of Logothetis et al. does not detract from their potential significance. Indeed, the stimulus conditions discovered by them—by effectively disengaging 'eye' rivalry—disclose yet another interesting, potentially important form of multistable perception. Many multistable phenomena, including conventional binocular rivalry, exhibit comparable temporal fluctuations, perhaps reflecting a fundamental property of neural dynamics (but not necessarily a common neural mechanism). It will be important to learn how 'stimulus' rivalry comes about and whether it can co-exist with eye rivalry. Preliminary ideas on these points can be found elsewhere (O'Shea, 1998).

Returning to the question of what rivals during rivalry, converging lines of evidence (Blake et al., 1979; Blake & Fox, 1974) implicate the 'eye' and not a given 'stimulus' at least under a wide range of conditions. However, 'eye' rivalry does not mean that an entire eye's view is dominant at a given moment during rivalry. On the contrary, dominance with large rival targets frequently appears patchy, with bits and pieces from the left- and right-eye views visible at the same time (Meenes, 1930; Blake, O'Shea & Mueller, 1992). Moreover, when one views an array of spatially distributed rival targets, it is possible for combinations of left-eye and right-eye targets to be dominant simultaneously (Kovács, Papathomas, Yang & Feher, 1996). These observations indicate that rivalry transpires within local regions of the visual field, and 'eye' rivalry means that only one eye or the other contributes to dominance within each of those regions.

Nor does 'eye' rivalry mean that observers consciously experience something other than the stimulus imaged in the dominant eye. Indeed, an observer does not know which eye is dominant at any given moment during rivalry—the observer 'sees' a stimulus without regard to its eye of origin. Moreover, neural activity associated with that dominant stimulus passes through all stages of visual information processing. Thus we would expect the dominant stimulus to activate higher cortical areas associated with the features of a dominant stimulus. So, for example, a face engaged in rivalry should activate regions in infero-temporal cortex when the face is dominant, as has been reported (Tong, Nakayama & Kanwisher, 1998). Descriptively speaking, binocular rivalry does involve a battle for domi-

nance between conflicting patterns, with the temporary loser suppressed from consciousness for several seconds at a time. But, importantly, suppression generalizes to any stimulus imaged in that suppressed eye, including the currently dominant one (Blake et al., 1979). The process underlying rivalry, unlike the human experiencing rivalry, does 'know' in which eye the dissimilar rival stimuli are imaged. Thus the search for rivalry's neurophysiological underpinnings should not overlook neurons whose signals retain some signature of their monocular origins.

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