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A common oscillator for perceptual rivalries?

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Abstract. Perceptual rivalry is an oscillation of conscious experience that takes place despite univarying, if ambiguous, sensory input. Much current interest is focused on the controversy over the neural site of binocular rivalry, a variety of perceptual rivalry for which a number of different cortical regions have been implicated. Debate continues over the relative role of higher levels of processing compared with primary visual cortex and the suggestion that different forms of rivalry involve different cortical areas. Here we show that the temporal pattern of disappearance and reappearance in motion-induced blindness (MIB) (Bonneh et al, 2001 *Nature* **411** 798 – 801) is highly correlated with the pattern of oscillation reported during binocular rivalry in the same individual. This correlation holds over a wide range of inter-individual variation. Temporal similarity in the two phenomena was strikingly confirmed by the effects of the hallucinogen LSD, which produced the same, extraordinary, pattern of increased rhythmicity in both kinds of perceptual oscillation. Furthermore, MIB demonstrates the two properties previously considered characteristic of binocular rivalry. Namely the distribution of dominance periods can be approximated by a gamma distribution and, in line with Levelt's second proposition of binocular rivalry, predominance of one perceptual phase can be increased through a reduction in the predominance time of the opposing phase. We conclude that (i) MIB is a form of perceptual rivalry, and (ii) there may be a common oscillator responsible for timing aspects of all forms of perceptual rivalry.

1 Introduction

Binocular rivalry is a form of perceptual rivalry that results when two different images are simultaneously presented to corresponding retinal locations of the left and right eye (Walker 1975; Wheatstone 1838). Under these conditions, the observer experiences rhythmical alternations between awareness and suppression of the two 'rivalling' images, even though the stimulus remains constant over time. A resurgence of interest in binocular rivalry has resulted from new investigations of its possible neural basis, including both single-unit recording data from monkeys (Leopold and Logothetis 1996; Sheinberg and Logothetis 1997) and scanning studies of humans (Lumer et al 1998; Polonsky et al 2000; Srinivasan et al 1999; Tong and Engel 2001; Tong et al 1998). To date, a variety of different cortical regions have been implicated in binocular rivalry (Lumer et al 1998; Srinivasan et al 1999). These experiments have raised new questions whether binocular rivalry can be considered an 'early' visual process (Blake 1989; Tong and Engel 2001) and tend to support alternative views that emphasise high-level, or top – down operations (Kovács et al 1996; Logothetis et al 1996; Walker 1978). In a recent position statement, representatives of both points of view reached a consensus that binocular rivalry is a complex, multilevel process that offers promise of illuminating cognitive functions such as attention and consciousness (Blake and Logothetis 2002). If binocular rivalry is multilevel, then a natural question concerns its relationship to other kinds of rivalries, where percepts oscillate in the face of invariant sensory input, just as they oscillate between the conflicting alternatives in binocular rivalry. It has been suggested repeatedly that all rivalries may share a common mechanism (Andrews and Purves 1997; Logothetis 1998; Wolfe 1996). We pursue that suggestion by comparing the timing of the perceptual oscillations in binocular rivalry with the timing of another, recently described, perceptual oscillation called motion-induced blindness, MIB (Bonneh et al 2001a).

This seemingly unrelated example of visual disappearance occurs when high-contrast stationary or slow-moving stimuli are superimposed on a global moving pattern (rotating cloud of dots). Under these conditions an observer will perceive the stationary stimuli to disappear for a few seconds before subsequently reappearing. While MIB is not usually considered to be a form of perceptual rivalry like the Necker cube, Rubin's face/vase, Boring's young/old woman, etc, the regular alternations between appearance and disappearance of the stationary targets invite a comparison with conventional rivalries.

2 Experiment 1: Stochastic properties of MIB

In order to investigate the hypothesis that MIB is a form of perceptual rivalry that shares the same underlying mechanisms as those responsible for binocular rivalry, we first undertook a qualitative study of the stochastic properties of MIB. As the duration of time between perceptual switches (alternation rate) has been shown to vary considerably between individuals (Pettigrew and Miller 1998), it was hypothesised that, while we would expect the pattern of MIB alternations to vary between subjects, each individual subject should report a similar temporal pattern of alternations for both MIB and binocular rivalry. Furthermore, as the distribution of phase durations for binocular rivalry has previously been shown to approximate a gamma distribution (Fox and Herrmann 1967; Levelt 1967; Walker 1975), we investigated whether MIB phase durations show a similar distribution.

2.1 *Methods*

2.1.1 *Subjects.* This study involved sixty-one subjects with normal or corrected-to-normal vision (6/9 or better) aged between 21 and 50 years. In total sixty-eight subjects were tested. Seven subjects were rejected from the study prior to analysis: five because they saw a combination of either patchwork or grid for more than 50% of the test period during binocular rivalry; and two because they were unable to perceive the disappearance of the dots in MIB. The subject population consisted of graduate students and employees at the University of Queensland. Fifty-four of the subjects were naïve to the paradigm and the aims of the experiment and the other fourteen were familiar with the experimental paradigm but were naïve to the aims of the study. All subjects volunteered their time. The study was approved by the University of Queensland Behavioural and Social Sciences Ethical Review Committee.

2.1.2 *Apparatus and stimuli.* For binocular rivalry, dynamic green vertical and horizontal lines were presented in a circular patch that subtended 1.5 deg of visual angle with a spatial frequency of 8 cycles deg^{-1} moving at 4 cycles s^{-1}. The stimuli were displayed on a monochrome computer monitor (green, P46 phosphor, persistence = 500 ns) and viewed from a distance of 3 m. In order to present the conflicting stimuli to the same retinal location of each eye, without the need for any training in fixation, we used a VisionWorks package and liquid-crystal shutters (Pettigrew and Miller 1998). The vertical and horizontal lines were alternately presented in rapid succession at a rate of 120 Hz. Subjects viewed the display through liquid-crystal shutters that blocked the stimulus presentation to the left and right eye in time with the alternating presentation of vertical and horizontal lines. Responses were recorded on a modified computer keyboard. Two raised buttons, one with a ridge aligned perpendicular to the observer and the other running from left to right, were placed on top of the B and V keys, respectively.

The MIB stimulus consisted of three yellow dots and a fixation cross, overlaid on a global moving pattern of 150 blue dots. The display was set on a black background and presented to subjects on a standard Macintosh (iMac) computer monitor, viewed from a distance of 60 cm. The yellow dots subtended 0.5 deg of visual angle arranged around a circle with a 4 deg radius to form a triangle, with a yellow fixation cross, 0.5 deg of visual angle, which had been added to the centre of the original display.

Except for the fixation cross, this was the same display as that used by Bonneh et al (2001a), which can be viewed at http://www.weizmann.ac.il/~masagi/MIB/mib.html. Responses were recorded on a standard computer keyboard and analysed with custom software (Matlab G-B Liu).

2.1.3 *Procedure.* During binocular rivalry, subjects were asked to report the predominance of vertical lines by pressing the V key, which had a pedestal with a vertically oriented ridge as a tactile cue. The predominance of horizontal lines was reported by pressing the B key, which had a pedestal with a horizontal ridge. If the subject experienced a combination of vertical and horizontal lines, either as a grid or a patchwork, for anything longer than a transitional period, they were instructed to press the space bar. The periods of space bar press were removed prior to analysis. As most subjects had no reports of mixed percepts (fifty-six of sixty-one subjects), and those that did showed a wide variation in rates, we feel that the removal of the space bar press was unlikely to introduce a criterion effect on the overall calculation of the individual's alternation rate. The data presented here, therefore, present the rates for binocular rivalry with mixed percepts excluded, as in previous studies (Pettigrew and Miller 1998).

During MIB, subjects were instructed to fixate on the cross while attending to the yellow dots and press the V key if any of the dots had disappeared and the B key if they could see all of the yellow dots in the display (B, if all of the dots were back).

Data for both binocular rivalry and MIB were collected, with the use of commercial software (Bireme.com.au) over a 10 min period consisting of 4×100 s trials, with subjects receiving a 30 s break between each trial. All tests were carried out in a dimly lit quiet room and the order of presentation for each of the tests was counterbalanced.

2.2 *Results and discussion*

The overall rate of alternation was found to vary greatly between subjects for both MIB (0.06 Hz – 0.84 Hz) and binocular rivalry (0.14 Hz – 1.46 Hz). However, despite the wide difference between individuals, there was a good correlation between the rate at which any given individual reported alternation between appearance and disappearance phases during MIB and the rate at which the same individual experienced alternations between rivalling horizontal/vertical percepts in binocular rivalry, $R = 0.7$ (figure 1). We feel confident that the rate measures do not merely reflect criterion effects, such as attention or variations in vigilance, as the rate of alternation has been shown to be robust in an individual, with test – retest correlation at $R = 0.8$ (Pettigrew and Miller 1998). Furthermore, any response lag, due to indecision, would be expected to affect both phases and therefore not to affect rate.

Representative phase-duration/frequency histograms for binocular rivalry and MIB further illustrate the intra-individual consistency and inter-individual variation in temporal pattern of alternations across the two phenomena, both in relation to the average

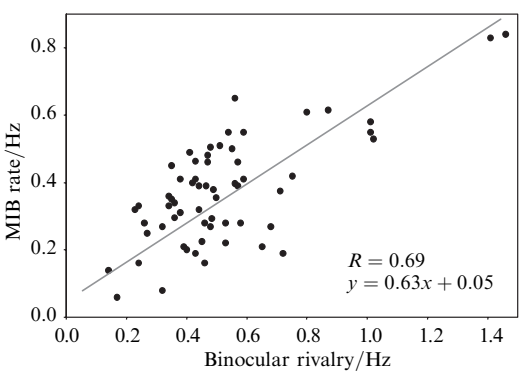


Figure 1. The correlation between the average rate of alternation for binocular rivalry and the disappearance/reappearance rate of MIB, for each subject.

phase duration and degree of deviation in phase durations (figure 2a). The similarity between binocular rivalry and MIB is equally evident when the distributions of phase durations are normalised for all subjects (figure 2b). In order to normalise the data, all appearance and disappearance phase durations were expressed as a fraction of the mean phase duration for each subject. The resulting frequency histogram shows that the distribution of relative phase durations for MIB approximates a gamma distribution ($R = 0.96$), where $f(x) = \lambda^r/\Gamma(r)x^{-1}\exp(-\lambda x)$, where $\Gamma(r) = (r-1)!$, R is the correlation coefficient, and λ and r are the values for the parameters which produce the gamma distribution that best approximates the normalised distribution of phase durations.

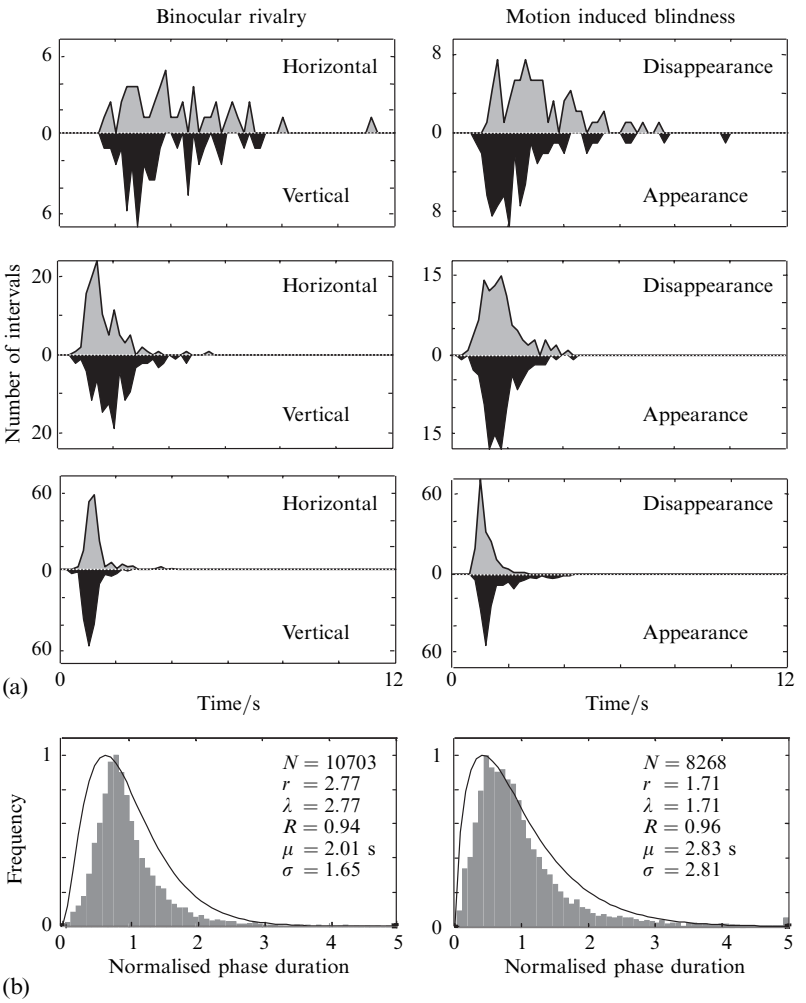


Figure 2. Temporal dynamics of binocular rivalry and MIB. (a) Frequency histograms of phase duration for binocular rivalry and MIB from three representative subjects. The histograms on the left show the number of reported horizontal (grey) or vertical (black) periods lasting between 0 and 12 s during binocular rivalry. The histograms on the right depict the subject's corresponding distribution of appearance (grey) and disappearance (black) periods. (b) Frequency histograms representing the normalised distribution of phase durations. The phase durations for binocular rivalry (left) and MIB (right) are expressed as a fraction of the mean phase duration for all sixty-one subjects. The phase durations for both binocular rivalry and MIB are approximated with a gamma distribution, $f(x) = \lambda^r/\Gamma(r)x^{r-1}\exp(-\lambda x)$, where $\Gamma(r) = (r-1)!$. N is the total number of phase durations, R is the coefficient of determination, μ is the mean phase duration for all subjects, σ is the standard deviation of the phase durations.

In fact, we found that the MIB distribution of phase durations was better approximated by the gamma distribution than by the distribution corresponding to the normalised dominance periods for binocular rivalry ($R = 0.94$).

Finally, the proposition of a common oscillator is strongly supported by the striking deviation from the usual gamma-like distribution of intervals that was observed for both phenomena in the responses of a subject who subsequently reported taking LSD 10 h prior to being tested. This subject showed a highly regular, multimodal response with harmonic intervals that were closely matched for both binocular rivalry and MIB (figures 3a and 3b). The extraordinary rhythmicity appears to be unique to the drug, since it has not been observed in over eight hundred subjects previously studied for binocular rivalry (J D Pettigrew, unpublished observation), nor was it replicated during subsequent retesting of the subject in the absence of this drug (figure 3c). Whilst it is not possible to determine, absolutely, the mechanism responsible for the effect, there are a number of features of the subject's response pattern that suggest that the observed results reflect

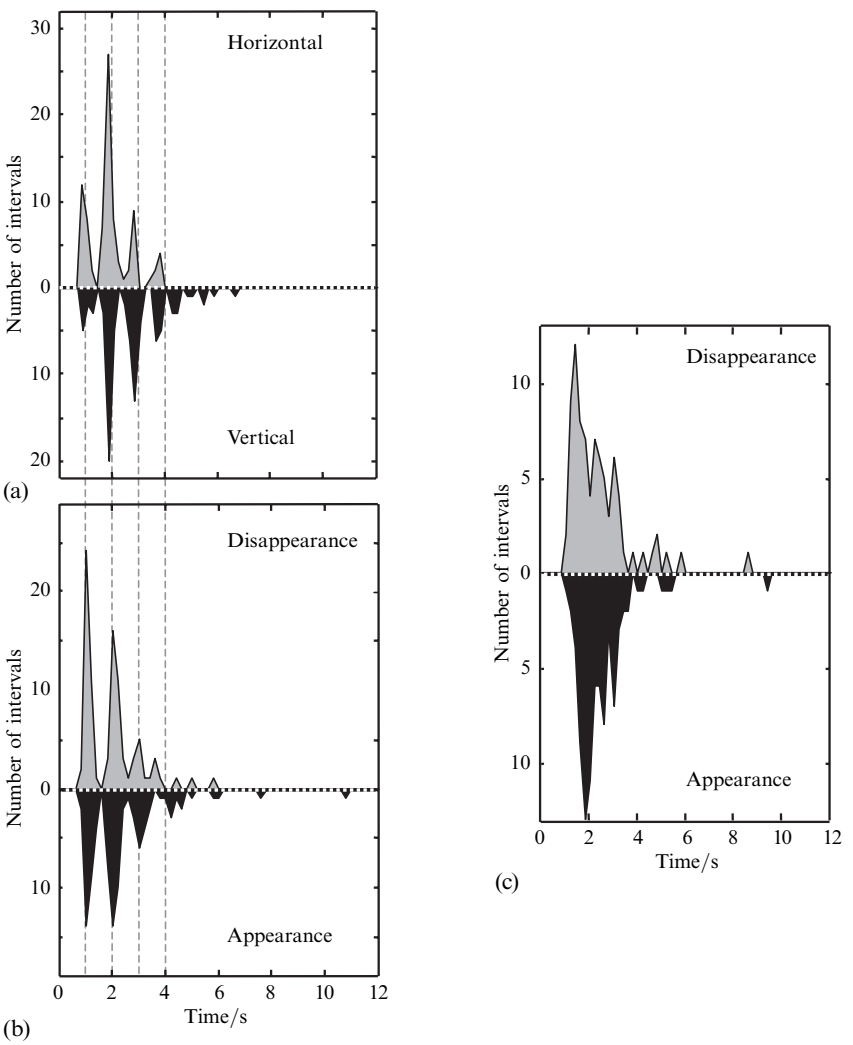


Figure 3. Frequency histograms corresponding to phase durations reported for (a) binocular rivalry and (b) MIB by a subject that had taken LSD 10 h prior to being tested. (c) Frequency histogram corresponding to phase durations reported for MIB by the same subject retested two months later, when the subject was not under the influence of LSD.

the subject's perceptual experience rather than a purely motor effect. For example, the subject reported a greater proportion of vertical lines in binocular rivalry (58%) and appearance phase in MIB (56%) in a manner consistent with the results of the other sixty subjects (vertical bias, $\mu = 52.3\%$, $\sigma = 6.1\%$, and appearance bias, $\mu = 57.1\%$, $\sigma = 13.7\%$). There was a slight shift towards shorter intervals (higher frequencies) in binocular rivalry (0.95 s, 1.9 s, 2.8 s) compared with MIB (1.0 s, 2.0 s, 3.0 s), which is in the same direction as the overall shift toward higher frequencies seen with binocular rivalry by all subjects.

While preliminary tests involving the related, but shorter-acting psychotomimetic, psilocybin, suggest that this increased rhythmicity occurs after the peak of drug activity (Vollenweider, Hasler, Carter, and Pettigrew, unpublished observations), it is premature to draw any general conclusions about the pharmacological basis of rivalry. Due to ethical limitations preventing the replication of the LSD finding, we present these preliminary observations here because we feel that the strikingly close match in numerous temporal details adds strong support to the claim that binocular rivalry and MIB share a common timing mechanism.

3 Experiment 2: MIB stimulus manipulation

It has repeatedly been shown that, manipulating the 'strength' of one of the rivalling figures through increases in motion (Breese 1909), contrast (Mueller and Blake 1989), and spatial frequency (Fahle 1982) will affect the overall predominance of that stimulus by changing the suppression, rather than dominance intervals, of that stimulus. This is often referred to as Levelt's second proposition for binocular rivalry (Levelt 1965). For example, if stationary vertical lines are presented to the left eye and stationary horizontal lines are presented to the right eye, introducing motion to the vertical line display will increase the proportion of time that the vertical lines are experienced. However, the duration of perception of vertical lines remains the same (eg a period of approximately 2 s before a switch to the other percept), while the duration of horizontal line dominance will be reduced (eg from 2 s to 1 s). Recently Hupé and Rubin (2002) showed that Levelt's second proposition applies to the dominance intervals of the bistable plaid percept, adding further support to the thesis elaborated here that different rivalries may share similar timing mechanisms, so we were motivated to explore the proposition with regard to MIB.

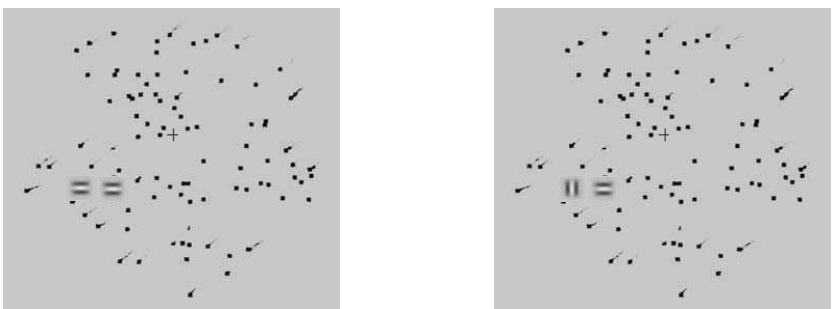
There are a number of problems with exploring Levelt's second proposition with regard to MIB. First, there is a fundamental problem in deciding how to match the phase of this asymmetrical alternation to the larger number of possibilities presented by the dual symmetrical suppression phases of binocular rivalry or other bistable percepts. It has already been shown that increasing the salience of the target stimuli during MIB will increase the duration of the MIB suppression phase (Bonneh et al 2001a). A second problem is that there may already be evidence that Levelt's proposition can be broken when there are high-order, 'contextual' effects that change the relative salience of the two alternative percepts in relation to the overall context (Sobel and Blake 2002; Bonneh et al 2002b). Here we consider an increase in the overall disappearance of the target as a sign of an increase in the target's 'strength'. Recent experiments with MIB with surface-completion effects and added stereo depth show the importance of the overall context in extending the disappearance or reducing its duration (Graf et al 2002). Added support for such a 'relative' interpretation of the 'strength' of the disappearing stimulus is more directly provided by experiments using transcranial magnetic stimulation (Pettigrew and Funk 2001). Bearing in mind the special difficulties in formulating the proposition in the case of this asymmetrical form of rivalry, we thought it important to determine whether the phase independence described by Levelt's second proposition might also apply to MIB. Here we show that

certain manipulations of the MIB stimulus can induce Levelt-type effects, further strengthening the similarity of MIB to other forms of rivalry. We show, first, that a pair of orthogonal gratings disappears to a greater extent than a pair of parallel gratings when presented along with a cloud of moving dots, thus supporting the interpretation that the orthogonal configuration has greater salience in the MIB effect; but then we show that this increase in disappearance is mediated by a reduction in the appearance time of the targets.

3.1 *Methods*

3.1.1 *Subjects.* This experiment involved a subset of nineteen subjects (eleven male and eight female) who participated in experiment 1. All subjects were naïve to the paradigm and the aims of the experiment.

3.1.2 *Apparatus and stimuli.* This experiment involved two MIB stimuli, similar to those used in experiment 1, except that the stationary yellow dots had been replaced with two adjacent Gabor patches located to the lower left side of the fixation cross. The patches subtended 1 deg of visual angle and had a spatial frequency of 2.5 cycles deg^{-1}. In one of the displays the patches were aligned collinearly with the dark/light grating running horizontally in each patch. The second condition was identical except that the orientations of the gratings in the patches were aligned orthogonally. The patch furthest to the left was rotated 90° such that the dark/light gratings ran vertically compared to the companion patch and compared to the first condition. In both displays the patches were superimposed on a global moving pattern of 150 black dots, set on a grey background (figure 4). This display can be viewed at http://www.weizmann.ac.il/∼masagi/MIB/mib.html. Responses were recorded on a standard computer keyboard.



(a) (b)

Figure 4. Stimuli used in experiment 2. (a) Collinear Gabor stimulus, with two adjacent Gabor patches aligned so that the dark/light gratings run horizontally. (b) Orthogonal Gabor stimulus, with two adjacent Gabor patches aligned so that the dark/light gratings of the left patch run vertically and the dark/light gratings of the right patch run horizontally.

3.1.3 *Procedure.* During the testing period subjects were instructed to fixate on the cross while attending to the Gabor patches and press the V key if either of the patches had disappeared and the B key if they could see both Gabor patches in the display.

As in experiment 1, data were collected with commercial software (Bireme.com.au) over a 10 min period consisting of 4×100 s trials, with subjects receiving a 30 s break between each trial. All tests were carried out in a dimly lit quiet room and the order of presentation for each of the tests was counterbalanced.

3.2 *Results and discussion*

Changing the alignment of the gratings from collinear to orthogonal was found to increase significantly the proportion of disappearance reported by the observers (collinear: $\mu = 41.82\%$, $\sigma = 10.59\%$; orthogonal: $\mu = 64.54\%$, $\sigma = 16.67\%$). On using a

repeated-measures analysis of variance this increase was found to be significant ($F_{1,18} = 63.75$, $p < 0.01$) (figure 5a). In line with Levelt's findings for binocular rivalry (Levelt 1965), this effect was not due to a direct increase in the duration of the disappearance phase (collinear: $\mu = 2.03$ s; orthogonal: $\mu = 2.02$ s), but rather a reduction in the duration of the appearance phase (collinear: $\mu = 4.12$ s, $\sigma = 1.92$ s; orthogonal: $\mu = 2.81$ s, $\sigma = 1.24$ s; $F_{1,18} = 23.61$, $p < 0.01$) (figure 5b). While the relative 'stimulus strength' of the collinear and the orthogonal Gabors is open to debate (eg it might be argued that collinear Gabors form a 'stronger' Gestalt), the results reported here show that the disappearance phase is relatively more prolonged for the orthogonal Gabors and that relative prolongation is mediated by a decreased time spent seeing the alternative percept, in accordance with Levelt's second proposition.

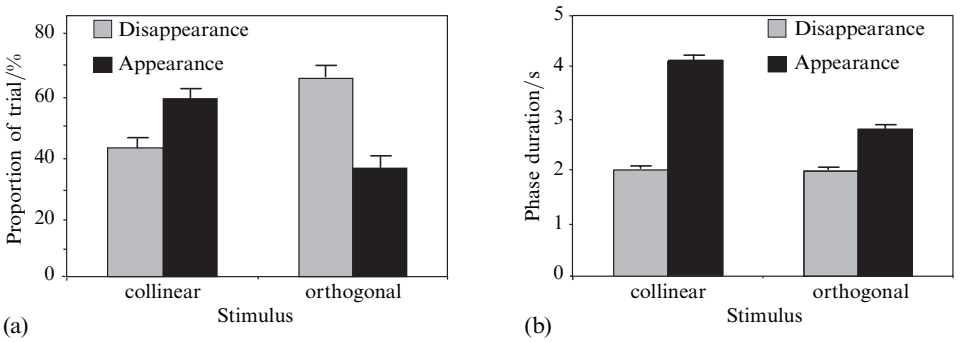


Figure 5. The effect of manipulations of MIB stimuli. (a) The proportion of the testing period that subjects reported the disappearance (grey) and appearance (black) increased significantly when the Gabor patches were rotated from collinear to orthogonal alignment. (b) The mean duration of the disappearance phase was found to be unaffected by the stimulus manipulations, while the duration of the appearance phases was reduced significantly in the orthogonal condition.

4 General discussion

A comparison of the temporal dynamics associated with MIB with those of binocular rivalry makes it clear that the two phenomena share more than a characteristic 'disappearance' of visual stimuli. Despite considerable variation between individuals, for any given individual the temporal pattern of alternations for MIB was consistent with that observed in binocular rivalry, both in relation to the average rate of perceptual alternation and the degree of deviation in phase duration. Furthermore, when the phase durations are normalised for all subjects, the distribution is approximated by a gamma distribution in a manner shown to be characteristic of binocular rivalry (Fox and Herrmann 1967; Levelt 1967). In previous studies the gamma-like distribution of phase durations and the Levelt effects had led people to emphasise the independence and unpredictable nature of successive rivalry alternations (Blake and Logothetis 2002; Fox and Herrmann 1967; Levelt 1966). We would like to point out that these characteristics are not inconsistent with our proposal that rivalry alternations are generated by an underlying rhythmical oscillator. While subjects showed variation in the duration of perceptual dominance phases, the distribution of phase durations was subject-dependent, being predictably reproduced across different stimuli (figure 2a). In other words, the notion of statistical independence of rivalry intervals is true only within an individual and breaks down when individuals of clearly different rivalry rate are compared under the same conditions. Furthermore, a process can be intrinsically rhythmical even if it is clearly affected by external factors. One only has to consider the influence travel can have on the intrinsically driven circadian rhythm (Meijer and Rietveld 1989).

With regard to the distribution of the normalised phase durations, we would like to stipulate that our use of the gamma statistics was largely driven by convention. We found that for both binocular rivalry and MIB our data could similarly be approximated by a log-normal distribution (data not shown). This is in line with Lehky's (1995) study showing that binocular rivalry alternations may be more accurately described by a log-normal distribution.

The postulate of an underlying shared oscillator is further supported by the observation of the same kind of rhythmic, multimodal pattern with both harmonic and forbidden intervals that was seen in a subject that subsequently reported having taken LSD 10 h prior to participation in the experiment. While we do not pretend to understand the mechanism of these changes, this observation raises interesting questions about the relation between the putative oscillator and the mode of action of the psychotomimetic that can only be addressed in more formal studies of this effect. In the meantime, we emphasise that whatever the exact neuropharmacology of the effect of LSD on the timing of rivalry alternations, the identity of the unique alterations in perceptual oscillation in both MIB and binocular rivalry argues strongly for a shared timing mechanism.

Further linking MIB to binocular rivalry, we show that it is possible to demonstrate the characteristic Levelt effect with a simple manipulation of the MIB stimulus. When the alignment of two adjacent Gabor patches is altered from collinear to orthogonal, the overall proportion of disappearance increases. This effect results not from an increase in the duration of the disappearance phase but rather from a decrease in the duration of the appearance phase.

The findings presented here provide new evidence that links binocular rivalry, a well-recognised and much studied example of perceptual rivalry, to the more recently described MIB, which had not previously been recognised as a perceptual rivalry. Apart from providing more support for the growing view that all perceptual rivalries may share a common underlying basis, some unusual features of MIB raise new questions about perceptual rivalry if we are to include it in this class of phenomena. In particular, we think that the striking disappearances of MIB, which occur without the usual 'symmetrical' reappearance of the alternative percept, raise the possibility that perceptual rivalries may be an inherently unobservable characteristic of everyday experience, rather than mere psychological curiosities. During the disappearance phase in MIB some components of the visual stimulus are temporarily inaccessible to consciousness. In everyday life, when the observer is not specifically attending to the disappearance and reappearance of target stimuli, such events would likely go unnoticed. If this speculation has any validity, perceptual oscillations may be a more ubiquitous aspect of normal perception than is apparent from their usual treatment as curiosities, and may reflect, for example, the inescapable ambiguities of perception (Purves et al 2000, 2001).

Our conclusion that MIB and binocular rivalry may share a common timing mechanism is consistent with studies linking other forms of perceptual rivalry (Gomez et al 1995; Maier et al 2001; Miller et al 2000; Walker 1976). Such results are difficult to explain with current 'low-level' models of binocular rivalry. In contrast, we believe that a shared timing mechanism that operates at the level of the whole hemisphere (Miller et al 2000; Pettigrew 2001) could explain the intra-individual similarity observed between the two phenomena, despite such marked inter-individual variation. Further, the suggested subcortical location of the oscillator is consistent with the diversity of cortical areas revealed by human scanning studies of rivalry (Lumer et al 1998; Tong and Engel 2001) and provides a common temporal framework for the multilevel aspects now accepted for binocular rivalry (Blake and Logothetis 2002).

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