

Visible binocular beats from invisible monocular stimuli during binocular rivalry

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When two qualitatively different stimuli are presented at the same time, one to each eye, the stimuli can either integrate or compete with each other. When they compete, one of the two stimuli is alternately suppressed, a phenomenon called binocular rivalry [1,2]. When they integrate, observers see some form of the combined stimuli. Many different properties (for example, shape or color) of the two stimuli can induce binocular rivalry. Not all differences result in rivalry, however. Visual ‘beats’, for example, are the result of integration of high-frequency flicker between the two eyes [3,4], and are thus a binocular fusion phenomenon. It remains in dispute whether binocular fusion and rivalry can co-exist with one another [5–7]. Here, we report that rivalry and beats, two apparently opposing phenomena, can be perceived at the same time within the same spatial location. We hypothesized that the interocular difference in visual attributes that are predominately processed in the Parvocellular pathway will lead to rivalry, and differences in visual attributes that are predominantly processed in the Magnocellular pathway tend to integrate. Further predictions based on this hypothesis were tested and confirmed.

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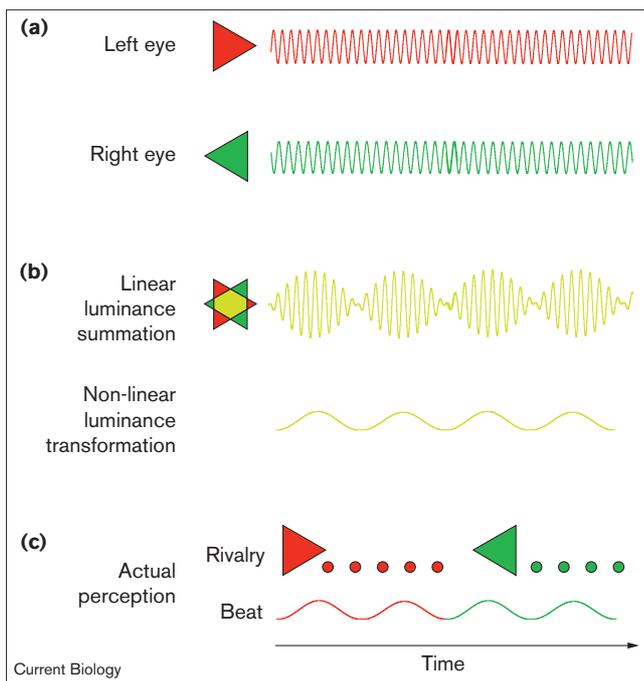
Results and discussion

Binocular rivalry represents a dissociation between the continuous presence of physical stimuli and the corresponding conscious experience, a property that has contributed to a recent return of interest in rivalry research [8–12]. Observations of the coexistence between rivalry and fusion go as far back as the 1930s when Creed reported the simultaneous perception of contour rivalry and background fusion [13], leading him to speculate, quite correctly, that different attributes are separately processed in the visual system. In addition, there have been several reported observations of stereopsis arising from differently colored contours while the colors themselves are engaged

in rivalry [14–16]. Random dot stereograms can be seen superimposed on, but not interacting with two orthogonal gratings engaged in rivalry, a phenomenon that Wolfe termed ‘trinocular vision’ [5]. Hastorf and Myro also reported that form and color rivalry could be de-coupled from one another ([17]; and see [5,18] for a general review). Nevertheless, there are also challenges to the coexistence of stereopsis and rivalry, particularly for the claim that they can be perceived at the same spatial location [6,7].

During the experiment, an observer’s left eye was presented with a red triangle facing left and the right eye a green triangle facing right (each side of the triangle extended 2.1° visual angle), and each was illuminated, respectively, with red or green light-emitting diodes (LEDs) from behind a plastic diffuser. At the same time, the luminance levels of the two stimuli were modulated as sinusoidal functions of time. It has been shown that differences in flickering frequencies do not lead to binocular rivalry [19], and, if the two frequencies are close to each other, observers with normal stereovision perceive a slow flicker amplitude modulation (beat) that corresponds to the difference between the two primary frequencies [3,4]. With this arrangement of stimuli, there were three possible perceptual outcomes. First, rivalry wins over integration: observers saw rivalry of the red and green stimuli because of the shape and color differences, and saw the flicker associated with each visible stimulus. Second, integration wins over rivalry: observers saw fusion between the two stimuli because flickers do not compete but integrate; this flicker fusion in turn captured color and shape, so the two stimuli fused as a whole. Third, there is coexistence between rivalry and integration: observers saw the two triangles rival each other in the sense that they saw one color and one shape at a time, but still saw integration of the flicker in the form of a visual beat. On average, subjects reported seeing rivalry 84% of the time when they were asked to indicate whether they perceived rivalry or fusion of the two stimuli. Thus, the second outcome could be ruled out.

The question was then whether subjects could see the beat when only one stimulus was visible. Subjectively, the answer was yes. Subjects could easily identify the luminance modulation of the beats during rivalry. To demonstrate this in a more objective way, we ran a forced-choice experiment. Three subjects (including the two authors and one naive observer) were dichoptically shown these two stimuli. During a two-alternative forced-choice experiment, the two LEDs modulated at 28 and 30 Hz in one 5 second interval and both at 29 Hz in the other

Figure 1

Schematic depiction of the co-occurrence of binocular rivalry and beats. **(a)** The left and the right eye were presented with two stimuli of different shapes and colors, both flickering at fast but slightly different frequencies. **(b)** Luminance modulation of the dichoptically presented stimuli could be integrated. For a linear integration, the result was an amplitude modulation, which could be perceived as a slow brightness modulation due to non-linear transformation. **(c)** Final percept: shape and color differences induced strong rivalry, yet the slow beat could be seen clearly even when one of the stimuli contributing to the beat was not visible.

5 second interval. Subjects were asked to make a forced-choice decision about which interval contained the beat. The results showed that subjects were able to identify the beat interval with near perfect accuracy (> 95% in more than 100 trials). Kolb and Braun recently showed that subjects have access to monocular information in binocularly fused images under forced-choice conditions, a phenomenon that they claimed represents a dissociation between performance and subjective confidence ([20], but see [21]). In the current experiment, beats were explicitly visible. Thus, subjects in our experiment were not performing at this high accuracy with low confidence. It would not be surprising if the stimuli presented to the two eyes were of the same color and shape [3,4]. In our experimental condition, however, the red and green opposite-facing triangles were rivaling one another. In other words, either the left or right eye's stimulus was visible. The fact that subjects could see the beat means that they must have integrated information from the suppressed stimulus.

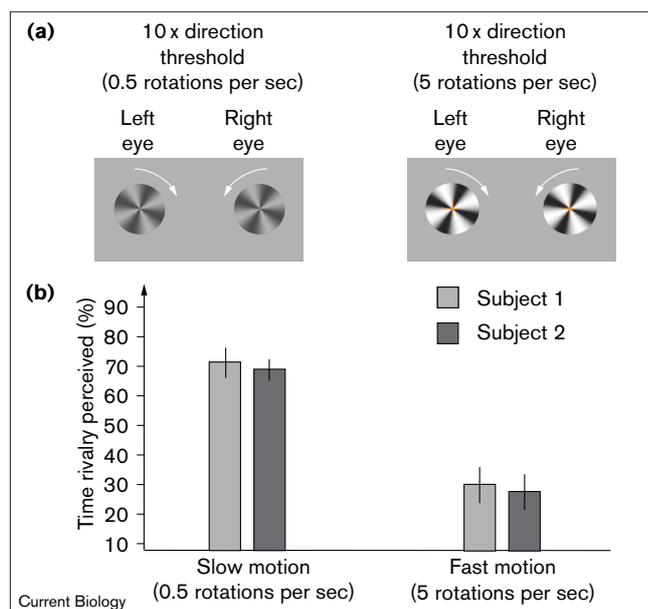
During the beat interval, although subjects saw only the left or the right eye's stimulus, the flicker information

(frequency and phase) from the suppressed/invisible stimulus still interacted with the visible stimulus. As a result, the emerged beat was seen despite the fact that one of the two sources for generating this beat was not visible (Figure 1c). In fact, observers felt that the beats were most obvious during the periods of complete suppression of one of the two stimuli, when only one eye's stimulus was exclusively visible!

This result is consistent with earlier observations of dissociation of visual attributes in rivalry and fusion. The nature of the attributes that are biased towards rivalry and fusion suggests a possible underlying mechanism for the uncoupling of rivalry and fusion phenomena. Fast flicker is more likely to be processed in the Magnocellular pathway, whereas color and shape information is preferentially processed in the Parvocellular pathway [22]. We propose that dissimilar information processed in the Magnocellular pathway is more likely to fuse, and information processed in the Parvocellular pathway is more likely to rival. There seems to be considerable evidence supporting this hypothesis. Properties that seem to support strong rivalry (for example, high-contrast spatial patterns) seem to be biased for the Parvocellular pathway, whereas properties that are more likely to result in fusion (for example, flicker and stereo disparity) seem to be biased for the Magnocellular pathway. Interestingly, Livingstone and Hubel came to the opposite conclusion [23]. They suggested that rivalry was a Magnocellular pathway phenomenon based on evidence that equiluminant chromatic stimuli were more likely to fuse and the rivalry process breaks down at high spatial frequencies. The reduction of rivalry at high spatial frequencies may be explained by the low retinal contrast at high frequency [24,25]. In fact, higher contrast sensitivity (thus responding to low contrast) is characteristic of the Magnocellular system. As for equiluminant chromatic patterns, Kulikowski reported strong rivalry using high-contrast chromatic stimuli [26]. Isoluminant stimuli through S-cones, presumably processed in the Parvocellular pathway, were also shown to generate perceptual rivalry [27]. Given the above consideration, the observation from Livingstone and Hubel could possibly be reconciled with our hypothesis that rivalry is mainly occurring in the Parvocellular pathway.

A necessary prediction from this Magnocellular/Parvocellular hypothesis is that if the contradicting information in the two eyes is mainly processed in the Magnocellular pathway, then one will see little or no rivalry. Although some of the earlier results provided partial support for this prediction, it has not been tested directly [28]. Andrews and Blakemore demonstrated that integration of motion signals from the two eyes can occur during form rivalry, but their experiment used only brief presentation, thus making it less convincing that rivalry was really involved [29,30]. In the current study, prolonged presentation was

Figure 2



(a) Stimuli configurations for the second experiment. Two radial gratings rotating in opposite directions were presented dichoptically to observers. In one condition, the gratings were rotated at slow speed (0.5 rotations per sec). In another, the gratings were rotated at a much faster speed (5 rotations per sec). All the stimuli were radial gratings with a radius of 2° , at spatial frequency of 4 cycles per rotation. Each observer measured his contrast threshold first for seeing the direction of motion at these two speeds. For observer TC, contrast thresholds were 1.52% and 2.27% for the slow and fast condition, respectively; for SH, the two thresholds were 1.78% and 6.77%. During the rivalry experiment, contrasts of the stimuli were set at ten times the threshold level. **(b)** Percentage of time during which observers perceived the two motion patterns in rivalry. At the slower speed, both observers perceived the two opposite motion in rivalry about 70% of the time, whereas at the higher speed, both observers saw rivalry about 30% of the time. The error bars are ± 1 SEM based on measurements over three sessions.

used so that the duration of the stimuli is no longer a limiting factor. As the Parvocellular pathway has a much slower temporal frequency response than the Magnocellular pathway, fast motion is predominantly processed in the Magnocellular pathway [22]. Thus, by manipulating the motion speed, stimuli can be generated so that the Magnocellular and Parvocellular pathway can be selectively biased. If rivalry is mainly a Parvocellular phenomenon, then rivalry perception should depend on the speed of motion when the two eyes are dichoptically presented with opposing motion.

Two radial gratings (4 cycles per rotation) were presented dichoptically, one rotating clockwise and one counter-clockwise. Monocular contrast threshold for perceiving the direction of motion was measured at two different motion speeds, 0.5 and 5 rotations per second. During the rivalry experiment, the pair of oppositely moving radial gratings

was presented at $10\times$ the threshold contrast. In five 2 minute sessions, subjects pressed a key whenever they saw rivalry. The proportion of time that they reported rivalry is plotted in Figure 2. It is apparent that, at high speed, opposing motion in the two eyes does not result in binocular rivalry as often as at a lower speed. At the slow speed, it may be the case that motion rivalry is based on the spatial misalignment of the stimulus rather than motion signal *per se* [31].

Color and shape are important contributors in determining object identities. Thus, when the stimuli presented to the two eyes are of different shape and color, it informs the visual system that the two eyes are seeing two different objects. However, luminance fluctuation often reflects the changes in lighting rather than difference in object *per se*. It makes intuitive sense that two different objects cannot occur in the same location in space, while it is possible that the same object may reflect more or less light to the two eyes. This may be the fundamental reason why the human visual system is developed in such a way that some inter-ocular differences result in binocular rivalry and some differences are simply integrated. The two parallel pathways seem to be well suited to deal with these separate task demands. Information processed in the Parvocellular system is more important in determining object identity, whereas information processed in the Magnocellular system contributes to the momentary appearance of an object.

Conclusions

We have demonstrated the coexistence of binocular integration and suppression. Specifically, binocular rivalry and binocular beats can be observed at the same time and in the same spatial location. This phenomenon could be explained by the independent processing of different visual attributes in the Parvocellular and Magnocellular pathways. Our results support the hypothesis that binocular rivalry is predominantly a property of the Parvocellular pathway. Furthermore, we propose that visual information from the Parvocellular pathway forms the core of visual awareness whereas information from the Magnocellular pathway serves to modify the final perceptual experience.

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