

Binocular rivalry in split-brain observers

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During binocular rivalry, visual perception switches between a stimulus viewed by one eye and a different stimulus viewed by the other. We studied rivalry in split-brain observers to test two explanations. Rivalry could reflect switching of activity between the cerebral hemispheres, or switching by a structure in the right frontoparietal cortex. From these two theories, we predict no rivalry when stimuli are presented to a split-brain observer's left hemisphere. Yet we found similar rivalry from the left and right hemispheres of the split-brain observers, consistent with switchings being mediated by low-level processes within each hemisphere.

Keywords: binocular rivalry, split brain, corpus callosum, human visual perception, consciousness

Introduction

Binocular rivalry occurs when one stimulus is presented to one of our eyes, and a different stimulus is presented to the other: one stimulus is seen and the other disappears. Every few moments, visual perception swaps between the stimuli. Perceptual awareness changes without any change in retinal stimulation. Understanding the neural substrates of binocular rivalry, then, would offer insights into the neural correlates of visual awareness.

Recent theories of binocular rivalry differ in the cortical regions involved in switching between stimuli and in the levels of visual processing at which rivalry arises. One, *interhemispheric-switching* (IS) theory, is that rivalry is processed at high levels of the visual system at which receptive fields cover the entire visual field. Each hemisphere adopts one of the rival stimuli; perceptual alternations reflect switching in dominance between the hemispheres (Miller, et al., 2000; Pettigrew & Miller, 1998). Another high-level theory, *RFPC* theory, developed from a study of rivalry using functional magnetic resonance imaging, is that the right frontoparietal cortex (RFPC) controls rivalry alternations through a mechanism involving perceptual selection (Lumer, Friston, & Rees, 1998).

Both theories seem to hold that if the two hemispheres of an observer were disconnected from one another, as with a split-brain patient, then rivalry should be disrupted. We can predict from IS theory that if one asked such an observer to describe rivalry, he or she would describe only the stimulus adopted by the left, verbal hemisphere. We can predict from RFPC theory that if one asked a split-brain observer to describe rivalry, the observer would describe something unlike rivalry (such as superimposition of the two stimuli), because the

left, verbal hemisphere is disconnected from the RFPC that normally selects the rival stimuli.

An older theory of binocular rivalry, *hypercolumn* theory, is that it is mediated at a low level of the visual system in which perceptual processing is essentially the same in the two hemispheres. Specifically, the level is that of cortical hypercolumns within the visual cortex (Blake, O'Shea, & Mueller, 1992; Mueller, 1990). Left-hemisphere hypercolumns cover the right visual field and right-hemisphere hypercolumns cover the left visual field. Switching of visibility is accomplished within each hypercolumn, but subject to cooperative influences from neighboring hypercolumns. From this theory we predict rivalry to be reported from the left hemisphere, and to be essentially identical to that reported from the right hemisphere.

We investigated rivalry in two split-brain observers who have had their corpora callosa sectioned to relieve epilepsy (Gazzaniga, Holtzman, Deck, & Lee, 1985). A major consequence of this surgery is that information presented to one hemisphere is largely inaccessible to the other. Because cells in the retina processing the left side of visual space project to the right hemisphere, and vice versa, these observers allow us to study rivalry in each hemisphere by restricting information to the left or right visual fields. Because each hand is almost exclusively controlled by the contralateral hemisphere, we can obtain perceptual reports from each hemisphere by asking such observers to press buttons with the hand ipsilateral to the stimulated field.

General Methods

Observers

Split-brain observers were the well-studied JW and VP. Each underwent two-stage callosotomy in 1979 to relieve epilepsy. JW is a right-handed male, and was 46 years old at the time of testing. We collected data from him in two sessions separated by several months. VP is a right-handed female, and was 47 years old at the time of testing. We collected only a few data from her in a single session. Both patients are highly experienced observers, although neither had reported on binocular rivalry prior to our experiments. Further details of their neurological histories are reported by Gazzaniga et al. (1985). We tested six intact-brain observers including us, all right handed, aged from 21 to 46 years. All observers had normal, or corrected-to-normal Snellen acuity in each eye, and good stereoacuity.

Apparatus

A Macintosh computer controlled two 17" Apple high-resolution color monitors viewed through a mirror stereoscope from 1 m. Observers gave responses using the "Z" and "X" keys to signal perception of the two rival stimuli with the left hand, and the "." and "/" keys with the right hand. To ensure that stimuli were lateralized to one visual field, we monitored eye movements using an iView eyetracker (software version 3.01; Sensomotoric Instruments, Needham, MA), comprising an infrared source, camera, and computer. This system has a resolution of approximately 0.5 deg.

Stimuli

There were two types of stimuli: rivalry and pseudorivalry. Each rivalry stimulus was presented constantly to one eye. Pseudorivalry stimuli combined two rival stimuli onto each monitor. During pseudorivalry, the contrast relationship between the two component stimuli changed smoothly between optical superimposition (both components visible at full contrast) and exclusive visibility (one of the components at full contrast and the other at zero contrast) according to preset schedules. The two stimuli were 2 cycle/deg sinusoidal gratings (0.8 contrast and 45 Cd/m² mean luminance). One was vertical and the other horizontal. They were displayed within circular fields of 2 deg diameter, on a background of 1.8 Cd/m². Surrounding each grating were white (81 Cd/m²) vertical fusion bars, 0.5 deg wide and 4 deg high, one to the left and one to the right of the centre of the screen by 2.5 deg. To present stimuli to the left or right hemisphere, observers were required to fixate a white X (81 Cd/m²) to the left or right of the center of the screen by 2 deg. Each arm of the X was 0.1 deg thick and 0.3 deg long. Testing took place

in a darkened laboratory with the stimuli providing the only light.

Procedure

First we trained observers with pseudorivalry stimuli. We gave the right and left hemispheres equal practice at each stage of training, and always trained the right hemisphere first. Once an observer was responding consistently to the known changes of the pseudorivalry stimuli, we went onto rivalry trials (see below). Again we made certain to test the left and right hemispheres equally. The start of each trial was signaled by a tone. For the stimuli to be presented, an observer pressed and then released two response keys simultaneously, using the first and second fingers of either the left or the right hand, depending on which hemisphere was being tested. Once the trial had begun, one key was to be pressed whenever horizontal bars were visible exclusively, and the other key whenever vertical bars were visible exclusively.

Trials lasted for 1 min in Experiment 1, and for 5 min in Experiment 2. Each trial was followed by a rest period of the same duration. After observers' first left-hemisphere trials, and after every subsequent trial, we asked them to describe their experiences of the stimuli. All observers described alternations in the visibility of the two stimuli, similar to those they had experienced with pseudorivalry, but they all commented on differences that are the hallmarks of real rivalry and are difficult to simulate in pseudorivalry, including composites and brief superimpositions of the two stimuli. JW's responses are particularly germane. After his first left-hemisphere rivalry trial, he said:

"Strange. They change right in the middle of the screen. They change from up-and-down [vertical] to right-to-left [horizontal]. Sometimes I see one on one side and the other on the other [he demonstrated with his fingers, showing vertical on the left and horizontal on the right]."

After training, we checked observers' eye fixation stability with the iView system. All kept their fixation within 0.5 deg of the fixation X for more than 95% of the time. Brief excursions further from fixation never approached the rival stimuli by more than 0.5 deg.

Experiment 1

We ran a balanced set of eight, 1-min rivalry trials in random order. These were formed by the factorial combination of eye/orientation (i.e., vertical to the left eye and horizontal to the right vs. the opposite) and hemisphere (right vs. left) repeated once.

Results and Discussion

Split-brain observers JW and VP reported rivalry from stimuli presented to either hemisphere. In VP's case, we have only six data, not enough to analyze statistically, although her means are similar to JW's. For the remaining observers, we employed three-factor analyses of variance (ANOVAs) with one repeated measure (orientation reported) using trials as replicates. We analyzed three dependent variables: exclusive visibility (the total time either response key was pressed), rate (the number of times either key was pressed), and period (the average time for which either key was pressed). We have summarized the data in Table 1.

From Table 1, we can see that JW's results are similar to those of the intact-brain observers. That is, he reported essentially normal rivalry from both hemispheres, as did VP. There are, however, some differences. JW had longer exclusive visibilities, $F(1, 8) = 6.78, p < .05$, faster rates,

Table 1. Means (and SDs) for Rivalry Measures from Each Hemisphere and F for the Difference

Observer	RVF/Left Hemisphere		LVF/Right Hemisphere		$F(1,4)$
Exclusive Visibility (s)					
JW1	23.88	(6.87)	22.80	(5.47)	0.07
JW2	38.02	(5.23)	22.92	(7.23)	16.61*
ROS	12.78	(6.07)	20.14	(4.47)	2.56
PC	42.23	(6.44)	43.25	(3.71)	0.06
MG	46.81	(8.75)	42.29	(6.17)	0.65
JT	49.77	(1.40)	41.85	(3.36)	17.54*
MM	44.72	(3.76)	44.16	(1.70)	0.05
Rate (presses per minute)					
JW1	6.00	(1.41)	8.25	(0.50)	7.36
JW2	12.50	(2.52)	17.25	(2.06)	10.94*
ROS	9.50	(5.07)	12.00	(1.41)	1.81
PC	23.00	(3.56)	22.25	(2.36)	0.09
MG	22.50	(2.38)	21.75	(1.89)	0.47
JT	30.00	(3.92)	23.50	(3.87)	6.63
MM	29.00	(0.82)	26.25	(1.71)	6.37
Period (s)					
JW1	5.09	(1.85)	2.47	(0.52)	11.94*
JW2	3.14	(0.41)	1.25	(0.31)	53.23**
ROS	1.35	(0.48)	1.55	(0.43)	0.60
PC	1.86	(0.39)	2.00	(0.33)	0.28
MG	2.16	(0.39)	1.99	(0.33)	0.56
JT	1.70	(0.26)	1.83	(0.25)	0.66
MM	1.57	(0.19)	1.69	(0.12)	0.88

Split-brain observer's two sessions are shown in boldface.

Note: * $p < .05$; ** $p < .01$.

$F(1, 8) = 87.36, p < .0001$, and briefer periods, $F(1, 8) = 15.66, p < .01$, in his second session than in his first. Such session-to-session variability is not unusual for JW, and may reflect differences in overall alertness or level of anticonvulsant medication between the two testing sessions. Administration of sedative drugs has consistently been found to reduce rivalry measures (Barany & Hallden, 1947; George, 1936; Platz, Uhr, & Miller, 1960; Ruttiger, 1963; Seedorff, 1956).

JW also showed some quantitative differences between the left and right hemispheres. He had longer exclusive visibility, slower rate, and briefer periods when stimuli were confined to his left hemisphere than to his right. VP showed similar differences. Only one intact-brain observer (JT) showed any difference between the hemispheres: longer exclusive visibility from the left hemisphere. We suspect that these quantitative differences reflect different reporting styles of the two isolated hemispheres (Ramachandran, 1994), rather than different processing of rival stimuli. The left hemisphere is supposed to gloss over inconsistencies such as brief periods, the right careful to report every change.

We found no evidence of the qualitative differences in rivalry between the hemispheres predicted by IS and RFPC theories. We looked for such qualitative differences with a fourth measure of rivalry in Experiment 2.

Experiment 2

Another way of quantifying rivalry is to plot the distributions of rivalry periods (Blake, Fox, & McIntyre, 1971; Cogan, 1973; Fox & Herrmann, 1967; Lumer et al., 1998). Such distributions have large positive skew, approximating gamma. Gamma distributions can be fitted to rivalry data by adjusting two parameters, λ and r , governing the variance and skewness respectively. We compared the fits to gamma distributions of periods from the left and right hemispheres of split-brain and intact-brain observers. Our method was similar to that of Experiment 1, except that trials lasted for 5 min so we could record many rivalry periods. We continued trials until we had a reasonable number of periods from both hemispheres.

Results and Discussion

We analyzed periods of 150 ms or longer. The distributions for split-brain observer JW and for intact-brain observer ROS are graphed in Figure 1. The parameters of the distributions for these and one other observer (IW) are summarized in Table 2. Figure 1 and Table 2 show that the shapes of the distributions approximate gamma, and are similar between the two hemispheres and across observers. This is despite large differences in the mean and SD of the distributions, with JW having the longest periods and IW the briefest. The

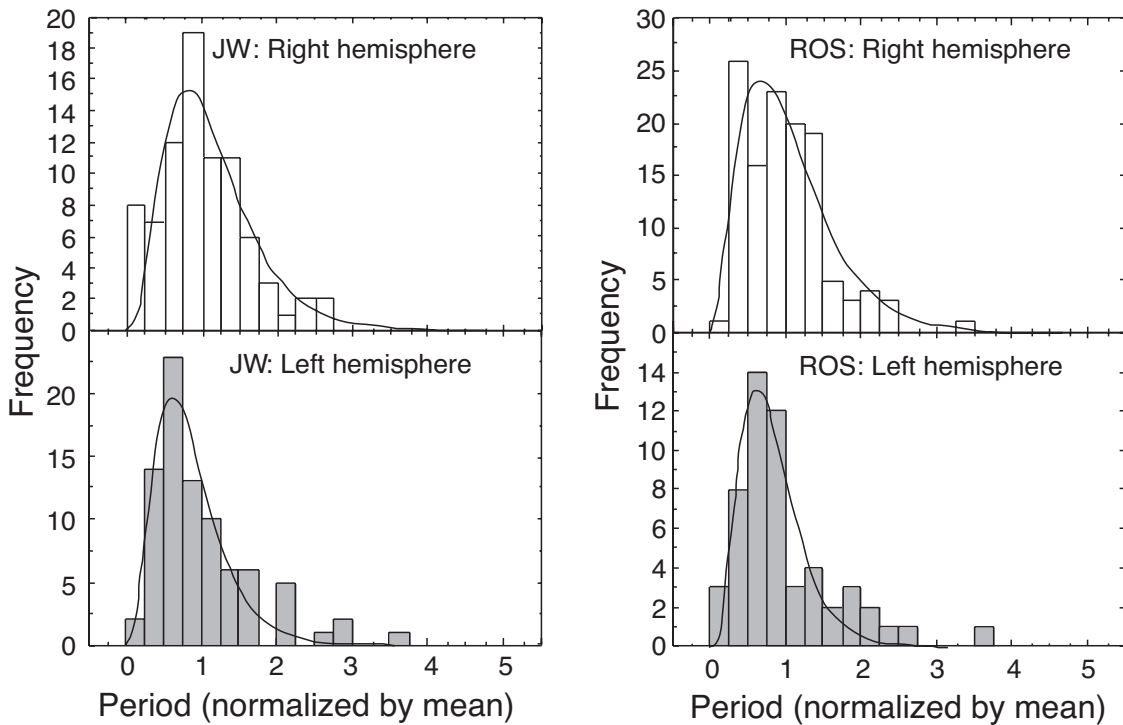


Figure 1. In the left panels are shown split-brain observer JW's distributions of rivalry periods and gamma distributions. In the right panels are shown intact-brain observer ROS's similar data and fits. In the top panels are shown results from the right hemisphere (white bars); in the bottom panels are shown results from the left hemisphere (gray bars). All four panels are remarkably similar.

fits to gamma yield R^2 values ranging between .91 and .996. The values of λ and r are within the normal range (Fox & Herrmann, 1967). We find no evidence in this experiment that the characteristics of rivalry differ qualitatively between the hemispheres of a split-brain observer.

General Discussion

We have found that rivalry between sinusoidal gratings is similar in the two hemispheres of split-brain observers. We (O'Shea & Corballis, 2001) have also recently found similar results with complex stimuli (faces and gratings of different colors), although in that study we could not monitor eye movements, nor did we measure the distributions of rivalry periods. Both studies yielded results consistent with rivalry being processed at a low level of the visual system at which each hemisphere covers only its own half of the visual scene, one of the tenets of hypercolumn theory.

From IS theory we predicted that when rival stimuli were confined to one hemisphere of a split-brain observer he or she would report one of them with no alternations. Yet we have consistently found these observers to report rivalry similar to that of neurologically intact observers. Miller suggested that rivalry could be processed within a hemisphere in split-brain observers but between hemispheres in intact-brain observers (Miller, 2001). As

Table 2. Parameters for Distributions of Rivalry Periods from Each Hemisphere.

Observer	RVF/Left Hemisphere		LVF/Right Hemisphere	
Mean (SD) (s)				
JW	6.17	(4.13)	6.37	(3.70)
ROS	1.92	(1.49)	1.76	(1.07)
IW	1.08	(0.48)	1.40	(0.66)
R^2 (N)				
JW	.95	(83)	.91	(82)
ROS	.93	(84)	.91	(121)
IW	.996	(321)	.994	(363)
λ				
JW	4.33		3.23	
ROS	5.11		2.72	
IW	5.75		5.52	
r				
JW	3.63		3.56	
ROS	4.15		2.81	
IW	5.56		5.27	

Split-brain observer is shown in boldface.

Pettigrew recognized, however, this weakens IS theory (Pettigrew, 2001). He preferred to attribute awareness of rival stimuli to the midbrain, which is not divided in split-brain observers. Doing so would take the theory out of the reach of our experiments, although it would then have to account for the neuroimaging evidence for cortical involvement in rivalry (e.g., Lumer et al., 1998; Polonsky, Blake, Braun, & Heeger, 2000).

From RFPC theory we also predicted no rivalry from the left hemisphere of split-brain observers because its direct connection to the RFPC had been cut. Yet both split-brain observers reported binocular rivalry from that hemisphere. If, however, there were some slower, weaker connection between the left hemisphere and the RFPC, perhaps via the midbrain, it could explain the quantitative differences we found between rivalry from the left and right hemispheres. It is also possible that there is a functioning switching apparatus in the left hemisphere, but that it is weaker than in the right hemisphere (Lumer & Rees, 1999). Either of these revisions of RFPC theory would be consistent with our results.

The one theory that does accommodate our data without revision is hypercolumn theory, in which each hemisphere carries out its own analysis of its half of visual space. That would put the processing of rivalry at a low level of the visual system, an idea for which there is mounting evidence (Polonsky et al., 2000; Tong & Engel, 2001).

Acknowledgments

R.O.S. was supported by Otago Research, Divisional, Departmental, and NZ-US CSP (00-CSP-44) grants, and by Paul Kaplan and Lisa Rothstein. P.C. was supported by a Human Frontiers Science Program Grant (RG0161/1999-B). We thank Malcolm Handley, Robin Gledhill, Barry Dingwall, Donovan Govan, and Mike Gazzaniga. Commercial relationships: none.

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