

16 Binocular Rivalry in the Divided Brain

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WHAT IS A DIVIDED BRAIN?

A person with a divided brain has had the corpus callosum, the large tract of fibers joining the two cerebral hemispheres, cut, usually to relieve epilepsy. This surgery does help control the epilepsy, but also has the fascinating side effect of revealing the lateralization of certain higher mental functions (Bogen and Gazzaniga, 1965; Gazzaniga, 1965; Gazzaniga, Bogen, and Sperry, 1962, 1965; Seymour, Reuter-Lorenz, and Gazzaniga, 1994). Specifically, the left hemisphere produces speech, understands speech, processes the right side of the sensory world, and controls the right side of the body. The right hemisphere understands spatial relations, understands some speech, processes the left side of the sensory world, and controls the left side of the body. Hereafter, we refer to people with such divided brains as split-brain observers.

In the intact brain, higher functions can be lateralized because the corpus callosum allows one hemisphere to access all of the sensorimotor world for that function. For example, spatial understanding can be lateralized to the right hemisphere because at that level of processing, the right hemisphere can represent the entire visual scene, both left and right of fixation.

WHY IS IT INTERESTING TO STUDY BINOCULAR RIVALRY IN THE DIVIDED BRAIN?

It is interesting to study binocular rivalry in split-brain observers to determine whether rivalry is a higher, lateralized function. There are two theories holding that critical aspects of rivalry are lateralized, and one theory—ours—holding that the rivalry mechanism is essentially duplicated at a low level of each hemisphere.

According to Pettigrew and colleagues (Miller, 2001; Miller et al., 2000; Ngo et al., 2000; Pettigrew and Miller, 1998), rivalry is processed at a high level of the visual system, possibly in inferotemporal cortex. At this level, they say, each hemisphere adopts one of the rival stimuli, rivalry reflecting alternations in activation of left and right hemispheres controlled by subcortical oscillators. Pettigrew et al. have some challenging evidence for their theory (detailed in chapter 15 of this volume). For example, they have found that squirting cold water into the right ear (cold caloric stimulation), a procedure that increases blood flow to the left hemisphere, can arrest normal rivalry alternations, perception presumably settling on whichever rival stimulus the left hemisphere has adopted. They also have found that disrupting the left hemisphere with transcranial magnetic stimulation (TMS) can trigger a rivalry alternation on about 50% of trials (this would be when perception is supported by the left hemisphere) but makes no change on the remaining 50% of trials (when perception would be supported by the undisturbed right hemisphere). In addition, they have found that people with bipolar disorder, whom they argue have slower subcortical oscillators, have slower rivalry alternation rates than people without such a diagnosis.

According to Lumer, Friston, and Rees (1998), rivalry is controlled by a structure in the right frontoparietal cortex. They showed a red, moving grating to one eye and a green face to the other while they measured fMRI activity. Observers pressed keys to signal their experiences of rivalry. Later, Lumer et al. played each observer a nonrival display that was perceptually the same as he or she had reported for rivalry. Observers again pressed keys, and had their fMRI activity measured. The only difference was that in one case any changes in appearance occurred because of rivalry, and in the other case any changes occurred because of physical disappearance of one of the monocular stimuli. When Lumer et al. subtracted one fMRI record from the other, they found a region of strong activation in the right frontoparietal cortex.

From both theories, we predict that no rivalry will be reported when stimuli are confined to the left hemisphere of a split-brain observer. In Pettigrew et al.'s theory, a split-brain observer should report only the stimulus adopted by the left hemisphere. In Lumer et al.'s theory, a split-brain observer should report something unlike rivalry, because the left hemisphere is cut off from the switching mechanism in the right hemisphere.

Our theory, however, is that rivalry is processed at a low level of the visual system, possibly within cortical hypercolumns of the primary visual cortex, V1 (Blake, O'Shea, and Mueller, 1992; Mueller, 1990). At this

level of the visual system, each hemisphere covers only its own half of the visual field. This means processing must be the same in the two hemispheres; otherwise, objects would appear to change as they moved from one side of the visual field to the other (which, as far as we know, has never been reported). If the rivalry mechanism is duplicated in each hemisphere, we predict similar rivalry from the left and right hemispheres of a split-brain observer.

WHO ARE OUR SPLIT-BRAIN OBSERVERS?

Our split-brain observers are JW and VP (Gazzaniga et al., 1985). (We have done most work with JW.) JW is male, now 50 years old; VP is female, now 51 years old. They had callosotomies in 1979. They are right-handed. They have good visual acuity in each eye and can see the depth in random-dot stereograms. They are extremely experienced psychophysical observers.

HOW DOES A SPLIT-BRAIN OBSERVER DESCRIBE RIVALRY?

We first tested our predictions by showing JW a pair of rival figures in a stereoscope (figure 16.1a). He described alternations between the stimuli, then said they looked like a black record with a white label alternating with a white record with a black label¹ (O'Shea and Corballis, 2001). Although we did not monitor JW's eye fixation in this experiment, this is such a beautifully poetic description that it could have come only from his left hemisphere. JW's right hemisphere is essentially mute.

Later, we conducted experiments in which we were able to monitor JW's fixation while presenting rival stimuli to the right or left field (to the left or right hemisphere, respectively). We also trained him and other observers, including VP, to report rivalry by pressing keys with the fingers of the right or left hand (controlled mainly by the left or right hemisphere, respectively). We asked observers to press one key whenever and for as long as they saw vertical with no trace of horizontal, and the other key whenever and for as long as they saw horizontal with no trace of vertical during 1-min trials. We first trained the observers to respond to pseudo rivalry changes (real changes to the stimuli that resembled rivalry alternations), and then tested rivalry. We monitored fixation with an eye tracker (SMI EyeView). We asked the observers to describe the stimuli after each trial.

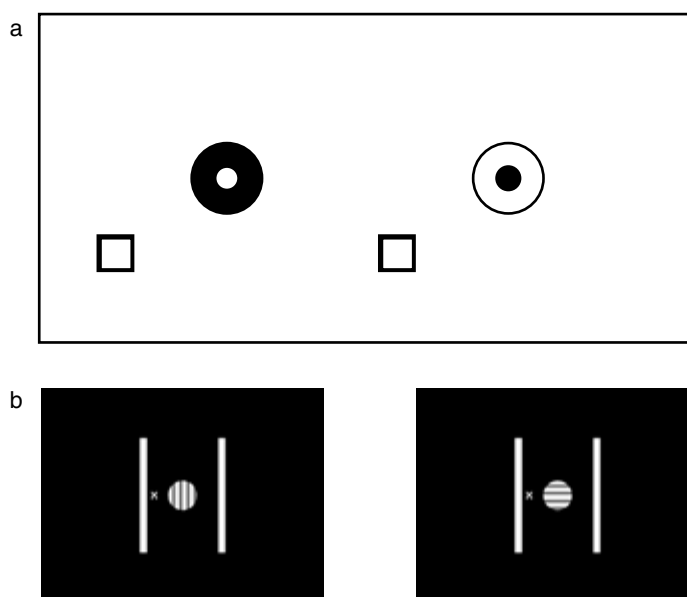


Figure 16.1 (a) Reproduction of the stimuli we displayed in a Telebinocular stereoscope to JW. The black ring was presented to the left eye and the white ring, to the right eye. When JW fixated the square, these images would be processed only by his left hemisphere (admittedly we could not monitor JW's eye fixation in this experiment). JW reported normal rivalry (O'Shea and Corballis, 2001). (b) Reproduction of the monitor screens viewed by the left eye and right eye through a mirror stereoscope in O'Shea and Corballis's (2003a) experiments. Each screen was $17.85^\circ \times 13.52^\circ$. The white bars assisted binocular alignment. Observers fixated the \times , in this case placing the rival gratings in the right field for processing by the left hemisphere. JW reported normal rivalry with these stimuli.

After JW's 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].

Later, in trials in which pseudo rivalry and real rivalry were interspersed, JW said of a left-hemisphere rivalry trial:

That's the one where there are two different ones the same time. Sometimes there would be [vertical] and [horizontal] together. Yuck! Sometimes I had one button halfway pressed while I decided what to do. Annoying because it changes so fast.

JW's reports leave us in no doubt that he experiences left-hemisphere rivalry in essentially the same way that intact-brain observers do. His

reports testify to the chaotic nature of rivalry alternations, which we were unable to simulate with our pseudo rivalry displays. JW's reports are problematic for theories that place any critical aspect of rivalry in the right hemisphere, but are consistent with our theory that the rivalry mechanism is duplicated in the two hemispheres.

After JW's right-hemisphere trials, he gave much simpler descriptions. He would say things like "OK" or "Lots of changes that time." These reports also came from his left hemisphere, which had not seen the stimuli. We suspect that JW's left hemisphere was able to report on the number of changes because it either had felt the left hand pressing the keys (through ipsilateral afferents) or had heard the keys being pressed (through the right ear). To learn more of the right hemisphere's experiences of rivalry, we have to turn to key-press data.

ARE THERE QUALITATIVE AND QUANTITATIVE DIFFERENCES OF RIVALRY FROM THE LEFT AND RIGHT HEMISPHERES?

To characterize rivalry fully, we analyzed four different aspects: exclusive visibility (the total time one response key or the other was pressed), rate (the number of key presses), period (the average time one response key or the other was pressed), and the distribution of durations of episodes of rivalry dominance. We have graphed the first three of these in figure 16.2.

As can be seen from figure 16.2, JW shows rivalry in both hemispheres that is similar to that of the intact-brain observer. (The intact-brain observer's results were similar to those of all the intact-brain observers we measured.) The only difference is that JW's periods from the left hemisphere are longer than those from the right. The other split-brain observer, VP, showed similar rivalry in the two hemispheres and longer periods from the left hemisphere (O'Shea and Corballis, 2001). This seems consistent with the response style of the two hemispheres: the right hemisphere is said to record every detail, whereas the left hemisphere is said to gloss over details (Ramachandran, 1994), perhaps ignoring brief departures from exclusive visibility. Our results do suggest that the qualitative experience of rivalry is the same in the two hemispheres.

In figure 16.3, we have plotted the distributions of durations of key presses from the left and right hemispheres of a split-brain observer and a representative intact-brain observer. These distributions have the classic gamma shape that is typical of rivalry (Blake, Fox, and McIntyre, 1971; Cogan, 1973; Fox and Herrmann, 1967; Lumer, Friston, and Rees, 1998).

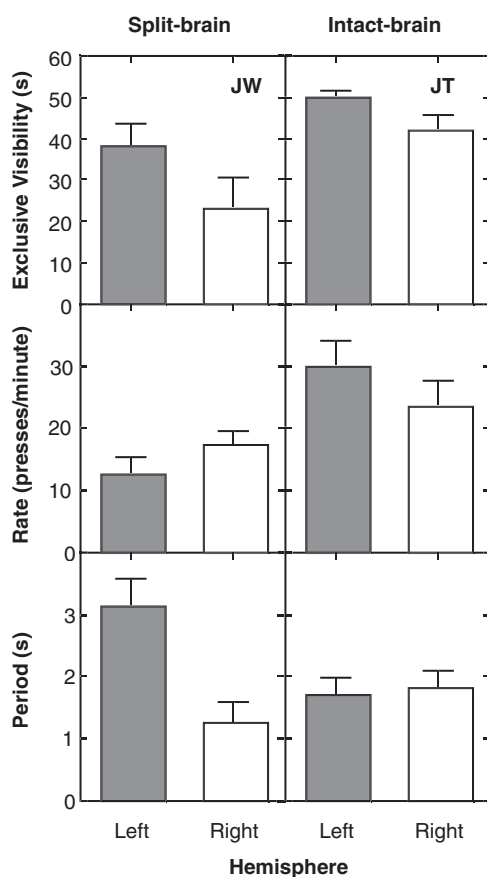


Figure 16.2 Quantification of rivalry from the left and the right hemispheres of JW and of an intact-brain observer in response to the stimuli illustrated in figure 16.1b. Error bars are 1 standard error. JW's rivalry is similar to that of the intact-brain observer, although with longer periods from the left hemisphere (O'Shea and Corballis, 2003a).

Despite JW's longer durations from the left hemisphere, there are no marked differences in the shapes of the distributions between the hemispheres of either observer, or between the observers. This measure also suggests that the qualitative experience of rivalry is the same in the two hemispheres.

In split-brain observers we found qualitatively similar responses to rival stimuli, whether presented to the left or to the right hemisphere. This was true for orthogonal achromatic gratings of different sizes and

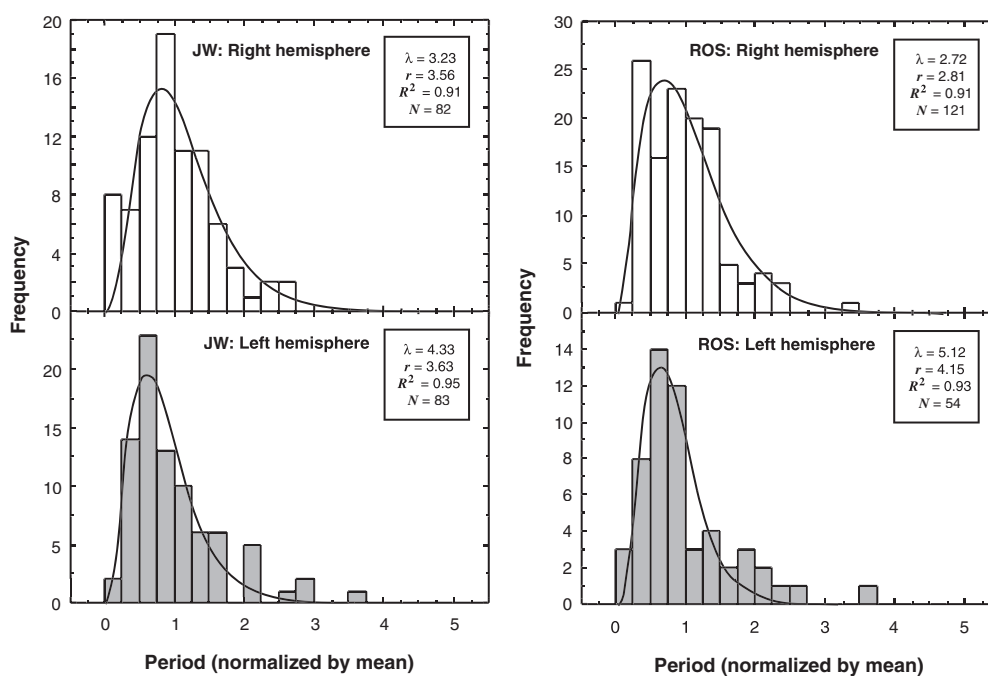


Figure 16.3 Distributions of durations of episodes of rivalry dominance from the left and the right hemispheres of JW and of an intact-brain observer in response to the stimuli illustrated in figure 16.1b. All distributions are remarkably similar, showing the typical gamma shape, and are well-fitted by gamma distributions whose parameter values are shown in the top right-hand corner (O'Shea and Corballis, 2003a).

eccentricities, oppositely colored gratings and faces (figure 16.4a; plate 6) (O'Shea and Corballis, 2001), and coherence stimuli (Diaz-Caneja; see Alais et al., 2000; figure 16.4b, see O'Shea and Corballis, 2003b). Coherence stimuli are particularly important because rivalry is between complete gratings that are distributed across the two eyes, implicating interocular visual grouping. That is, we found similar interocular grouping in each of JW's hemispheres.

We also showed JW rival gratings on both sides of fixation and had him track rivalry on both sides simultaneously by pressing two keys with the left hand and two keys with the right hand. He was able to do this effortlessly, something that defeated all our intact-brain observers. His rivalry from the two hemispheres was essentially independent.

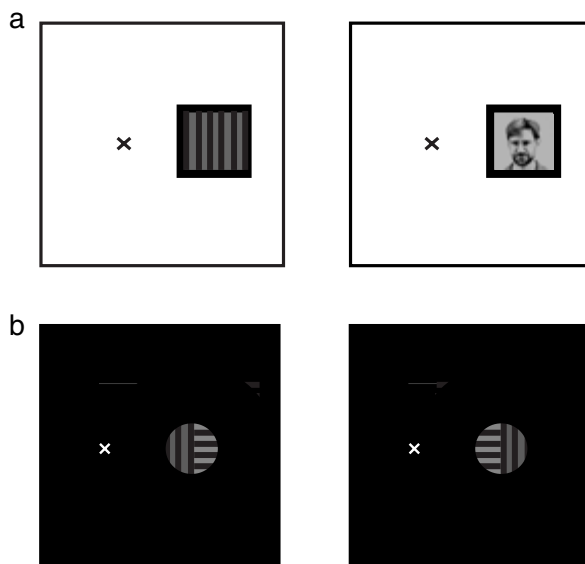


Figure 16.4 (a) Stimuli presented, one to each eye, to test whether rivalry between complex stimuli, similar to those used by Lumer, Friston, and Rees (1998), might yield differences between JW's hemispheres. No qualitative differences were found (O'Shea and Corballis, 2001). (b) Example of Diaz-Caneja-type rivalry stimuli. Occasionally, perception is of a red vertical grating alternating with a green horizontal grating, showing that visual grouping can operate across the eyes to yield coherence rivalry. JW reported similar coherence rivalry from his two hemispheres (similar to that of intact-brain observers) (O'Shea and Corballis, 2003b). See plate 6 for color version.

DOES HAVING A CORPUS CALLOSUM MAKE ANY DIFFERENCE TO RIVALRY?

JW has an intact anterior commissure, so one might argue that the coordination of the two hemispheres required by Pettigrew et al. and Lumer et al. is accomplished via this pathway. This seems unlikely; in split-brain observers the only function ever demonstrated for the anterior commissure is exchange of olfactory information (Gazzaniga, 2000).

Nevertheless, to examine whether there were any interhemispheric effects on rivalry in our split-brain observer, we used a technique invented by Alais and Blake (1999). They presented pairs of gratings to one eye, and sets of random dots to the same locations in the other eye, for 60 sec. The gratings and dots engaged in rivalry. Alais and Blake asked their observers to press one key whenever one grating appeared (with no trace of

dots), and another key whenever the other grating appeared (with no trace of dots). They computed joint predominance: the time both keys were pressed, divided by the total time either or both keys were pressed. This yielded a dimensionless number ranging from 0 (when neither key was pressed at the same time as the other) to 1 (when both keys were always pressed at the same time).

Using their technique, Alais and Blake manipulated the grouping characteristics of the gratings. That is, gratings could be collinear (so that the bars would join up if extended; good grouping), parallel (intermediate grouping), or orthogonal (minimal grouping). Also, the gratings could be confined within one visual half-field, and hence one hemisphere, or distributed between two half-fields, hence occupying two hemispheres. The essentials of their design are illustrated in figure 16.5.

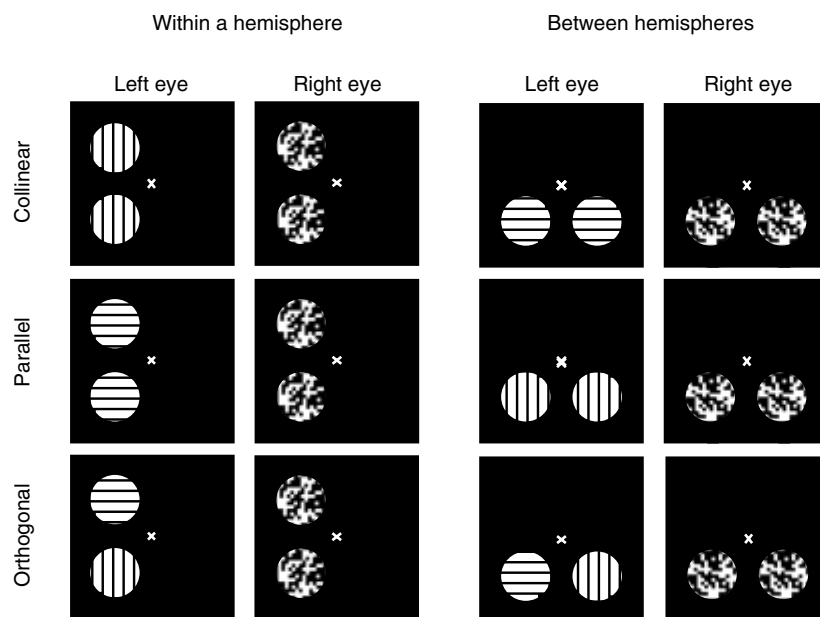


Figure 16.5 Illustration of stimuli similar to those used by Alais and Blake (1999) and by us (O'Shea and Corballis, 2003b). The left panels show stimuli confined within a hemisphere, in this case the right (left field). Left-hemisphere stimuli also were tested. The right panels show stimuli distributed between the hemispheres. In this case, stimuli are displayed below the horizontal meridian; stimuli above the horizontal meridian also were tested. The top panels show gratings that are collinear. The middle panels show gratings that are parallel. The bottom panels show gratings that are orthogonal (HV). The other possible arrangement of orthogonal gratings (VH) also was tested.

Alais and Blake discovered that the joint predominance of the gratings was greater for collinear and parallel gratings than for orthogonal gratings, whether within or between hemispheres. They also calculated joint predominance expected from independent rivalry within each region. All conditions except for orthogonal gratings were significantly greater than this predicted level. Grouping effects on rivalry between hemispheres presumably depend on communication across the corpus callosum.

We conducted a similar experiment on JW and some intact-brain observers. For our experiment, we scaled up all dimensions of the stimuli to keep the pairs of rival stimuli off the area of nasotemporal overlap. We first trained our observers to respond to pseudo rivalry changes in the stimuli, and we monitored eye fixation. Our results were similar to Alais and Blake's for intact-brain observers (one shown on the right of figure 16.6).

Critically, JW's results (see the left panel of figure 16.6) also were similar when the stimuli were confined within one hemisphere. In these conditions, there were no differences in joint predominance from the left or right hemisphere. When the stimuli were distributed between the hemispheres, however, there were no significant grouping effects at all. Thus, we finally ran an experiment in which JW's lack of a corpus callosum made a difference to his rivalry.

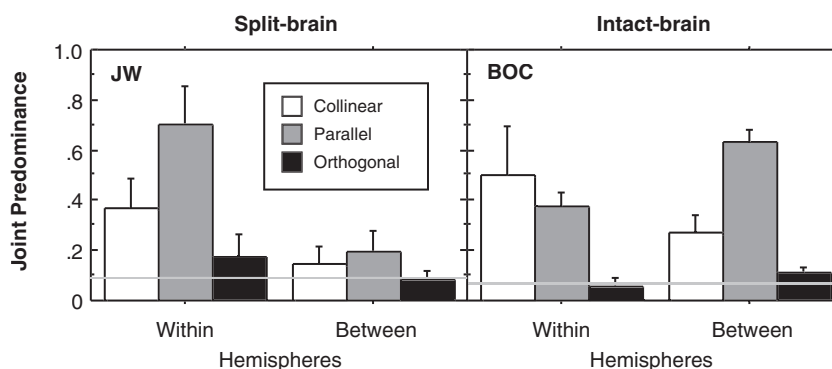


Figure 16.6 Joint predominance of JW and of an intact-brain observer in response to the stimuli illustrated in figure 16.5 (O'Shea and Corballis, 2003b). Error bars are 1 standard error. The gray line shows the level of joint predominance expected from independent rivalry in the two regions. JW shows the effect of visual grouping when the rival gratings were confined within one hemisphere, but no effects of visual grouping when the gratings fell in different hemispheres. The intact-brain observer's results are similar to those of Alais and Blake (1999), with grouping effects within and between hemispheres.

JW's lack of any interhemispheric grouping of rivalry rules out any major contribution to rivalry of the anterior commissure, because otherwise Pettigrew et al. would have to hold it responsible for his normal visual-grouping effects with Diaz-Caneja stimuli (figure 16.4b) but not for between-hemisphere visual grouping effects (figure 16.6). It also demonstrates that JW has normal rivalry in each hemisphere, and that the effects of grouping are the same in each hemisphere. The effects of grouping probably arise from lateral interconnections between adjacent regions of the cortex analyzing adjacent regions of the visual field (e.g., Das and Gilbert, 1995; Gilbert, 1992). In intact-brain observers, these lateral connections must cross the corpus callosum to give grouping between the hemispheres. These connections are cut in JW's case.

To summarize this section, we find similar rivalry in each hemisphere of a split-brain observer, consistent with the rivalry mechanism being duplicated in each hemisphere. We doubt that such duplication has developed following the callosotomies of our split-brain observers. We think duplication represents the normal state of affairs in the intact brain, required because each hemisphere's rivalry mechanism covers only half of the visual field.

HOW DO WE RECONCILE PETTIGREW ET AL.'S DATA WITH OURS?

We think there are alternative explanations of Pettigrew et al.'s results. For example, cold caloric stimulation and TMS may simply alter the rivalry mechanism within the hemisphere controlling responses to centrally presented rivalry stimuli. We note that Pettigrew et al. always presented the same rivalry stimulus to the same eye, thereby confounding stimulus with eye. It is possible that cold water in one ear or a magnetic pulse to that side of the head affects stimuli imaged in the eye on that side. Pettigrew et al.'s finding of slower alternations in people with bipolar disorder could be from the mood-stabilizing drugs used to control the disorder in the majority of Pettigrew and Miller's (1998) patients (see also Miller et al., 2003). Although the effects of these drugs on rivalry have never been specifically tested, other drugs, such as sedatives and alcohol, slow rivalry alternations (e.g., Platz, Uhr, and Miller, 1960; Ruttiger, 1963; Seedorff, 1956).

In any case, there is one major problem for Pettigrew et al.'s theory: rivalry composites. When rival stimuli cover large areas of the visual field, for much of a trial one sees small patches of one stimulus dynamically intermingled with small patches of the other. Only rarely do all the patches of one image coalesce to yield an episode of exclusive visibility. In

Pettigrew et al.'s terms, there must be many independent switches, one for each location in the visual field. The area over which rivalry dominance spreads, scales with spatial frequency in the same way as with fusion and stereopsis (O'Shea, Sims, and Govan, 1997), and binocular phenomena that Pettigrew may agree are processed in V1 (Barlow, Blakemore, and Pettigrew, 1967). In Pettigrew et al.'s terms, the independent switches must scale with spatial frequency. The area over which rivalry dominance spreads also matches that of receptive fields of V1 neurons at different eccentricities (Blake, O'Shea, and Mueller, 1992). In Pettigrew et al.'s terms, the independent switches must scale with eccentricity like V1 neurons, instead of neurons higher in the visual system, which have much larger receptive fields. The properties of the visual system revealed by rivalry composites require Pettigrew to duplicate many of the properties of V1 wherever the switches are located in the brain. It is more parsimonious to put the switches in V1. This is essentially our contention.

HOW DO WE RECONCILE LUMER ET AL.'S DATA WITH OURS?

We think there are complex reasons for Lumer et al.'s finding rivalry-related fMRI activity in the frontoparietal cortex, regions supposed to be involved in allocating spatial attention. When we used Lumer et al.'s technique for producing pseudo rivalry, we noticed that the observer's task of pressing keys was much simpler than when the alternations were produced by rivalry. As JW's verbal reports attest, real rivalry is much more chaotic than pseudo rivalry; it is much more difficult to decide when to press keys. We are quite prepared to believe that the attention devoted to deciding when to press a key during rivalry involved the frontoparietal cortex.

It is also worth pointing out that Lumer et al.'s technique for producing pseudo rivalry actually involves rivalry. To produce an episode of pseudo rivalry dominance, say of red verticals, Lumer et al. increased the contrast of that stimulus to one eye while decreasing the contrast of the other stimulus to the other eye. During the changes, therefore, both stimuli were presented dichoptically, yielding the conditions for binocular rivalry. When the change was over, the red grating was presented to one eye and a gray field to the other, yet only the grating was perceived. Hering (1964) called this form of binocular rivalry contour dominance. It has now come to be called permanent suppression (e.g., Ooi and Loop, 1994). It is possible (although we think it unlikely) that the brain regions for conventional

rivalry and permanent suppression differ at the level of the frontoparietal cortex.

In any case, in later research Lumer and Rees (1999) also found enhanced fMRI activity to rivalry in the left frontoparietal cortex, although this seemed weaker than in the right. According to the logic of Lumer et al., if each hemisphere has its own switching mechanism, we would predict no, or small, differences in rivalry in the isolated hemispheres—just what we found.

CONCLUSIONS

Split-brain observers have essentially normal rivalry in each hemisphere; this is true even when the components of rival stimuli are distributed across the eyes (Diaz-Caneja stimuli) or across the visual field (Alais and Blake's stimuli).

In JW's case, there are no effects on rivalry of grouping between hemispheres, suggesting that grouping effects in intact-brain observers are mediated via the corpus callosum with little, if any, contribution from the anterior commissure.

Our results present difficulties for the theories of Pettigrew et al. and of Lumer, Friston, and Rees (1998) but are consistent with ours that the rivalry mechanism is duplicated in each hemisphere. Duplication is necessary at the level of the visual system at which each hemisphere processes only its own half of the visual field, namely, at low levels such as V1.

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NOTE

1. A *record* was a flat disk of vinyl into each side of which a spiral groove had been pressed. By rotating the disk on a record player, a needle picked up vibrations encoded in the path of the groove that were amplified as sounds, usually music. That is, a record was an analog sound recording device (similar to a CD), popular in JW's and ROS's youth.

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