

# Paradoxical Interhemispheric Summation in the Split Brain

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## Abstract

■ We measured simple reaction time (RT) to light flashes, presented either singly or in pairs, in two people who had undergone callosotomy, one person with agenesis of the corpus callosum, and 17 normal subjects. The three split-brained subjects' RTs were decreased to bilateral pairs beyond predictions based on a simple race between independent unilateral processes, while those of the normal subjects were actually longer than predicted by the race model. This effect

was present whether the bilateral pairs were in mirror-image locations or not, but was not present when the pairs were presented unilaterally. Since summation does not depend on close spatial correspondence, and also occurs when inputs are staggered in time, we suggest that it is due to cortical projection to a subcortical arousal system, and is normally inhibited by the corpus callosum. ■

## INTRODUCTION

When people must respond as quickly as possible to visual targets, their reaction times (RTs) are typically faster when two targets appear simultaneously in left and right visual fields than when single targets appear in just one visual field. This is an example of *redundancy gain*, in which RT is speeded by the presence of an extra redundant target. In neurologically normal people, the effect is generally consistent with a simple race model, in which the two targets set up a race for the control of response and the faster process wins (Corballis, 1998; Reuter-Lorenz, Nozawa, Gazzaniga, & Hughes, 1995). In this case, there is no need to postulate any neural interaction between the two stimuli.

Somewhat paradoxically, there is evidence for an enhanced redundancy gain, in which the race model is clearly violated, in most subjects lacking the corpus callosum through surgery (Iacoboni, Ptito, Weekes, & Zaidel, 2000; Corballis, 1998; Marzi et al., 1997; Reuter-Lorenz et al., 1995), and at least some subjects with callosal agenesis (Iacoboni et al., 2000; Corballis, 1998). There is also evidence that the enhanced redundancy gain occurs only if the targets are in opposite visual fields, and not if double targets appear in the same visual field (Iacoboni et al., 2000; Reuter-Lorenz et al., 1995). These results do imply interhemispheric interaction in the split brain, despite the absence of the main interhemispheric fiber tract. Further, violation of the race model was largely eliminated when the stimuli were

equiluminant with the background in those with surgical section of the corpus callosum, consistent with the expectation that the redundancy gain in the split brain is mediated subcortically, perhaps by the tectal commissure. Rather surprisingly, however, the effect was if anything enhanced by equiluminance in a subject with agenesis of the corpus callosum (Corballis, 1998).

One possibility is that the interaction giving rise to neural summation occurs at the level of the superior colliculi (Iacoboni et al., 2000), and it has been further suggested that the effect may depend on homotopic mapping between the two colliculi (Corballis, 1998). Evidence for homotopic (or mirror image) mapping between the colliculi comes from other studies of subcortical interactions between the two visual fields (Tomaiuolo, Ptito, Marzi, Paus, & Ptito, 1997; Corballis & Sergent, 1992; Zihl & von Cramon, 1980; Singer, Zihl, & Poppel, 1977). If this is so, then we might expect the effect to occur when pairs of stimuli are presented in opposite visual fields in mirror-image locations, but not when they are in non-mirror-image locations. A primary aim of this study was to test this prediction.

We tested two men (M. E. and J. W.) who had undergone callosotomy for the relieve of intractable, multifocal epilepsy, one man (R. B.) with agenesis of the corpus callosum, and 17 people with no known neurological deficit. White disks were flashed against a black background either singly or in pairs. The possible locations were at the corners of an imaginary square, in the upper left, lower left, upper right, and lower right visual fields. Single stimuli appeared equally often in each of these locations, and double stimuli appeared equally

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often in all six possible pairs of locations. This allowed us to determine whether interhemispheric redundancy gain differed between the upper and lower fields, whether interhemispheric redundancy gain occurs when the stimuli located in the same visual field and are therefore relayed to the same hemispheres, and when they are diagonally opposite and are therefore not in mirror-image locations.

## RESULTS

There were very few errors. Out of 500 signal trials, the normal subjects missed an average of 3.18 signals with the left hand and 3.18 with the right hand, and out of 50 blank trials, they incorrectly responded an average of 0.76 times with the left hand and 1.0 times with the right hand. M. E., J. W., and R. B. missed 3, 9, and 9 signals out of 500 with the left hand, and 2, 3, and 3 with the right hand, respectively. The numbers of incorrect responses on blank trials were 4, 0, and 0 with the left hand and 1, 1, and 1 with the right hand, respectively. Table 1 shows overall RTs for each hand and each visual field.

Redundancy gain is best revealed, not by mean RTs, but by cumulative distributions. At some given time  $t$  after a stimulus has been presented, let  $P_i$  be the probability that a response has occurred to a stimulus ipsilateral to the responding hand,  $P_c$  the probability that a response has occurred to a stimulus contralateral to the responding hand, and  $P_{ic}$  the probability that a response has occurred when stimuli appear simultaneously in both visual fields. Redundancy gain would imply that  $P_{ic}$  is larger than  $P_i$  or  $P_c$  across all values of  $t$  in which responses occur. According to a race model, however, if the stimuli in the bilateral condition independently race to control the response, then we expect the following:

$$P_{ic} = P_i + P_c - P_i P_c \quad (1)$$

Consequently, if  $[P_{ic} - (P_i + P_c - P_i P_c)]$  is greater than zero, we can say that the redundancy gain exceeds that predicted by the race model, and some interhemispheric neural interaction is implied. We can assess the violation of the race model by plotting this expression

over  $t$ , and where the expression exceeds zero we can infer neural summation.

Cumulative probabilities were computed for each double-stimulus combination, along with the two corresponding single-stimulus conditions, for each subject. For instance, when the double-stimulus condition consisted of top left and bottom right stimuli (“down” diagonal), the appropriate single-stimulus conditions were top left and bottom right. For each possible combination of double-stimulus presentations, then, all three distributions were pooled, and RTs cumulated in bins of 5, starting with the 5 shortest RTs, then the 10 shortest, and so on, to give a total of 30 bins (150 trials) for each combination. Within each bin, cumulative frequencies were allocated to each condition, and divided by 50 to give probabilities  $P_{ic}$ ,  $P_i$ , and  $P_c$ . The expression  $[P_{ic} - (P_i + P_c - P_i P_c)]$  was then calculated for each bin, and was plotted for each double-stimulus condition. These plots are shown in Figure 1, individually for the three split-brained subjects and averaged for the normal subjects.

For the normal subjects, it is clear that the averaged curves lie below zero, indicating that responses to double stimuli are less than predicted by the race model, perhaps because the corpus callosum creates an attentional divide between hemispheres, slowing down the race. Standard deviations are shown on the graph and occasionally rise above the zero axis, especially for the shorter RTs, and in fact some subjects did exceed the race model on some occasions.

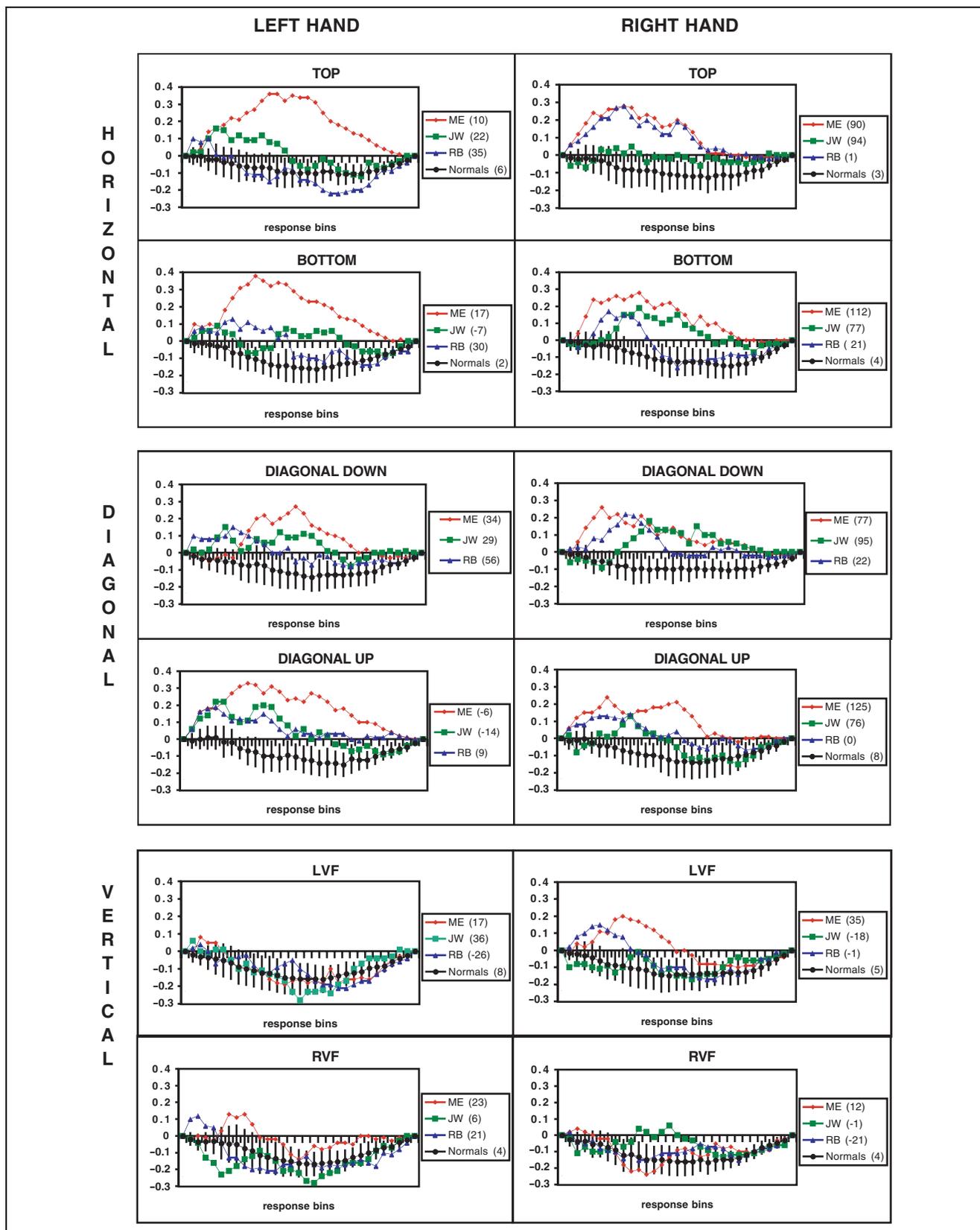
To provide an overall measure of redundancy gain,  $[P_{ic} - (P_i + P_c - P_i P_c)]$  was summed over the 30 response bins. Table 2 shows the means for each of the different arrangements; namely, horizontal pairs, diagonal pairs, and vertical (unilateral) pairs. For the normal sample, the overall mean was significantly less than zero [ $F(1,16) = 190.37, p < .001$ ]. There was also a significant difference among the different arrangements [ $F(2,32) = 4.18, p = .024$ ], and paired comparisons showed the mean for unilateral presentations to be significantly ( $p < .05$ ) lower than those for bilateral presentations. We also tested specifically for a difference between upper and lower horizontal arrangements, since a previous report showed the redundant target effect to be greater in the lower than in the upper field (Miniussi, Girelli, & Marzi, 1998), but the difference was not significant [ $F(1,16) = 1.73, p = .207$ ], and was in any case in the opposite direction (mean =  $-2.16$  for the upper field,  $-2.70$  for lower field).

It is clear both from Figure 1 and Table 2 that, when stimuli were in opposite fields, redundancy gain was much greater for the split-brained subjects than for the normals, and in most cases violated the race model, implying interhemispheric neural summation. In all cases shown in Table 2, the split-brained subjects were at least two standard deviations above the normals for bilateral arrangements, and J. W. and R. B. were within

**Table 1.** Mean RTs (msec) for Each Hand and Visual Field

Subjects	Left Hand	Right Hand	LVF	RVF
M. E.	325	301	357	317
J. W.	388	369	412	378
R. B.	317	289	306	320
Normals	295 (30)	297 (32)	299 (32)	299 (31)

Standard deviations in brackets for normal sample. Left- and right-hand RTs include bilateral stimuli.



**Figure 1.** Plots of expression  $[P_{ic} - (P_i + P_c - P_i P_c)]$  over 30 response bins, shown for each combination of paired stimuli. Top four panels represent horizontal arrangements, middle four diagonal arrangements, and bottom four vertical (unilateral) arrangements. Vertical bars are standard deviations. Bracketed numbers in the legends are CUDs.

**Table 2.** Mean CUD (msec) and Redundancy Gain (RG)

Conditions	Measure	Subjects			
		M. E.	J. W.	R. B.	Normals
Horizontal	CUD	57.4	46.5	21.8	3.87 (5.67)
	RG	4.39	0.23	-0.30	-2.43 (0.80)
Diagonal	CUD	57.4	46.5	21.8	3.87 (5.67)
	RG	3.20	0.62	0.99	-2.36 (1.02)
Vertical	Bottom-top	22.0	5.5	6.25	5.84 (6.22)
	RG	-1.40	-2.89	-2.48	-2.97 (1.00)

Standard deviations shown in brackets for normal group. Average CUDs for horizontal and diagonal conditions are identical, since they are based on the same means (rearranged). There is no CUD for the vertical conditions, and the values shown are differences in RT between bottom and top locations.

one standard deviation of the normals for unilateral arrangements. M. E. showed by far the greatest violations of the race model, and both M. E. and R. B. showed some violation under the unilateral condition. On the whole, however, the data confirm previous evidence for interhemispheric neural summation in the split brain, and show little evidence for “intra-hemispheric” summation in these subjects.

The interhemispheric summation effect for these subjects was clearly present in the diagonal arrangements, implying that mirror-image placement is not necessary to produce the effect. There is also evidence that the effect is present when stimulus pairs are in non-mirror-image locations in the same horizontal plane (Roser & Corballis, 2002). These data are counter to the suggestion that the effect may depend on symmetrical placement of paired stimuli (Corballis, 1998).

The enhanced redundancy gain in the split-brained subjects with bilateral presentation is especially paradoxical when it is considered that interhemispheric transfer is much slower in these subjects than in the normals. Interhemispheric transfer time can be estimated from RTs to unilateral stimuli by subtracting the RT of responses to stimuli contralateral to the responding hand from those ipsilateral to the responding hand (Poffenberger, 1912). This difference is known as the crossed-uncrossed difference (CUD). Values of the CUD for the individual conditions are shown in the legends in Figure 1, and averaged for each of the horizontal and diagonal arrangements in Table 2; they confirm earlier evidence that the CUD is an order of magnitude larger in callosotomized people than in normal people, while in those with callosal agenesis, it lies somewhere in between (Forster & Corballis, 1998; Iaconi & Zaidel, 1995; Aglioti, Berlucchi, Pallini, Rossi, & Tassinari, 1993). Given that interhemispheric transfer is considerably slowed in the split brain, one might expect neural summation with bilateral presentation to be reduced rather than enhanced.

It might be thought, though, that the enhanced redundancy gain is an artifact of the lengthened CUD, which would lower the value of  $P_c$  relative to  $P_i$ . This in turn would tend to increase the value of the expression  $[P_{ic} - (P_i + P_c - P_i P_c)]$ , perhaps implying that the redundancy gain as measured by this expression is artificially inflated. For this logic to hold, however, it must be assumed that the interhemispheric processes underlying the CUD does not affect responses to bilateral stimuli, but merely adds to the RT to unilateral stimuli in the field contralateral to the responding hand. This could occur if, for instance, neural summation occurs prior to the interhemispheric transfer that leads to the lengthening of response to unilateral stimuli in the field contralateral to the responding hand.

There is little evidence that this was the case, and if anything redundancy gain tended to be increased when the CUDs were “shorter” and the values of  $P_c$  were correspondingly higher. For each of the split-brained subjects, redundancy gain summed over response bins was correlated with absolute CUD over the eight conditions shown in the top eight panels of Figure 1. In each case, the correlation was negative, although in no case did it reach significance on a two-tailed test: for M. E.,  $r = -.633$ ,  $p = .092$ ; for J. W.,  $r = -.233$ ,  $p = .578$ ; and for R. B.,  $r = -.598$ ,  $p = .117$ . Nevertheless, the consistent negative correlations suggest that redundancy gain may be enhanced to a slightly greater extent when the CUD is short than when it is long. This belies the notion that enhanced redundancy gain is simply an artifact of prolonged CUD, but suggests that information from the crossed stimulus can more readily interact with that from the uncrossed stimulus the shorter the CUD. Even so, it is clear from Figure 1 that there was still considerable enhancement of the redundancy gain when the CUD was long.

When broken down by hand, as in Figure 1, CUDs are partly confounded by differences between the hemispheres in processing time. For instance, if processing of a stimulus is faster in the left than in the right hemisphere, this difference would add to the CUD for the right hand, and subtract from the CUD for the left hand. Both M. E. and J. W. show longer CUDs for the right hand, consistent with faster processing in the left hemisphere, as confirmed by shorter overall RTs to stimuli in the right than in the left visual field (see Table 1)—in the case of M. E. this can be attributed at least in part to a large lesion in the right prefrontal cortex. Yet both subjects show violations of the race model when responding with the right hand, even though transfer of information from the right hemisphere is considerably delayed. Conversely, R. B. shows somewhat longer CUDs for the left hand, due to faster processing by the right hemisphere (see Table 1), perhaps because he is a left-hander. R. B. also shows some violation of the race

model when responding with the left hand, despite relatively slow transfer.

## DISCUSSION

These results confirm the enhanced redundancy gain in the split brain, and verify that it depends on bilateral stimulus presentation. The results do not confirm earlier suggestions that it might depend on mirror-image stimulation, since the effect was as marked with diagonal arrangements as with horizontal ones. This might be taken as evidence against the view (Iacoboni et al., 2000; Corballis, 1998) that the neural summation causing the effect depends on interhemispheric integration at the level of the superior colliculi. Visual stimuli are mapped topographically onto the superior colliculi, and the present data suggest that the effect is independent of stimulus topography, provided only that the stimuli are in opposite visual fields. It is also unlikely that redundancy gain depends on interaction via the anterior commissure, since the effect was earlier shown to be present in two subjects (L. B. and N. G.) in whom the anterior commissure, as well as the corpus callosum, was sectioned (Iacoboni et al., 2000; Corballis, 1998).

One possibility is that the effect depends on subcortical arousal mediated by the reticular formation. The present results suggest that the effect is only weakly dependent on CUD, being slightly reduced when the CUD is long. Other evidence has shown that redundancy gain in the callosotomized subject J. W. was only weakly attenuated when the two stimuli were staggered in time, implying a temporal integration window of at least  $\pm 50$  msec<sup>2</sup>. These findings suggest the accumulation of arousal level, with both stimuli feeding into an arousal process with low temporal resolution, so that it spreads over a relatively long time window. This might have the effect of speeding the processing of both stimuli through feedback to the cortex, and so speeding the “race” for control of the response. Functional MRI recorded from one split-brained subject showing interhemispheric neural summation suggests that this activation may occur in the extrastriate cortex (Iacoboni et al., 2000).

What remains to be explained is why the effect is not present in normal subjects. One possibility is that neural summation effectively acts as an “and” gate, requiring input from both hemispheres (Reuter-Lorenz et al., 1995). This does not act to speed responses, but releases a chronic inhibition. In normal subjects, rapid interhemispheric transfer ensures that the “and” gate operates even when there is only one stimulus, but in the split brain, it can only operate when stimulation is bilateral. This might explain why both M. E. and J. W. responded more slowly than the normal controls—this is shown in Table 1, where the RTs for the LVF and RVF exclude bilateral stimuli. This slowing, however, may be attributed simply to generalized results of surgery, especially

in the case of M. E. who also underwent section of the right prefrontal cortex. The RTs of R. B. were not markedly slowed, yet he showed an enhanced redundancy gain.

An alternative possibility is that the corpus callosum normally acts to inhibit processing of crossed stimuli, so that they have a diminished role in the activation of arousal. In the normal subjects, redundancy gain was on average at least two standard deviations below that predicted by the race model (Table 2). This suggests some suppression of processing that is accomplished both within hemispheres in the case of unilateral pairs, and between hemispheres in the case of bilateral pairs. This suppression is presumably cortical, since it is absent in the split brain when the stimuli are bilateral. This arousal might also be related to the allocation of attention, since there is some evidence that split-brained subjects, unlike normal subjects, can allocate attention simultaneously to the two visual fields (Ivry, Franz, Kingstone, & Johnston, 1998; Luck, Hillyard, Mangun, & Gazzaniga, 1994).

## METHODS

### Subjects

There were three subjects lacking the corpus callosum. Two of them, J. W. and M. E., had undergone two-stage surgical section of the corpus callosum for the relief of intractable epilepsy, J. W. in 1979 and M. E. in 1989. The anterior and other commissures were left intact. M. E. had previously undergone removal of an epileptic focus in the right prefrontal cortex. J. W. was 46 years old and M. E. was 30 years old at the time of testing, and both are right-handed.

The third subject lacking the corpus callosum was R. B. a 24-year-old man with agenesis of the corpus callosum. He is left-handed, with a score of  $-14$  on a scale ranging from  $-24$  to  $+24$  (Briggs & Nebes, 1975). He was subjected to MRI examination in 1988 at the age of 12 after complaining of headache and visual fatigue. This showed congenital absence of the corpus callosum along with enlarged lateral ventricles, as is common in callosal agenesis. He has no history of epilepsy.

Seventeen neurologically intact people volunteered to take part. One was a graduate student at the University of Verona, and the rest were recruited from staff and graduate students at the University of Auckland and their friends. There were eight men and nine women, and they ranged in age from 19 to 51 years, with a mean of 29.8 years. Two were left-handed according to the Edinburgh Handedness Inventory (Oldfield, 1971), with Laterality Quotients of  $-100$  and  $-43$ , while the rest had quotients ranging from 50 to 100.

The ages of the normal subjects spanned those of the split-brained subjects, but no attempt was made at individual matching. Nevertheless, correlations between

the redundancy gain scores obtained by summing the expression  $[P_{ic} - (P_i + P_c - P_i P_c)]$  over response bins and the age, sex, and handedness of the normal subjects were computed for each of the 12 conditions shown in Figure 1. Of the 36 correlations thus obtained, only one was significant, that between laterality quotient and the redundancy gain score obtained under the lower-field horizontal arrangement (second panel down on the right in Figure 1) with right-hand responses; this correlation was  $-.59$  ( $p = .013$ ). The mean correlation with sex was  $.038$ , where the positive sign indicates slightly greater redundancy gain for women than for men; the mean correlation with age was  $.003$ ; and the mean correlation with handedness was  $-.102$ , where the negative sign indicates slightly higher redundancy gain with increasing left-handedness. These correlations suggest that the enhanced redundancy gains shown by the split-brained subjects are very unlikely to be due to the sex, age, or handedness of the subjects.

### Apparatus and Stimuli

All stimuli were presented on a 17-in. video graphics adapter (VGA) monitor controlled by an IBM-compatible computer, which was also used to collect responses. The stimuli were presented against a uniform dark gray background with a luminance of  $5.27 \text{ cd/m}^2$ . The subjects sat with their eyes 57 cm from the screen, at which distance 1 cm subtended a visual angle of  $1.0^\circ$ .

The stimuli consisted of white circular discs of diameter 63 mm. They were centered at four possible locations at the corners of an imaginary square measuring 11.76 by 11.76 cm. That is, each disc was 5.88 cm to the left or right of a central fixation cross and 5.88 cm above or below the cross. These locations may be identified as top left (TL), bottom left (BL), top right (TR), and bottom right (BR). Each stimulus was presented for 100 msec.

There were 11 presentation conditions. In the four single-disc conditions, the discs were presented singly in each of the four locations (TL, BL, TR, and BR). In the six double-disc conditions, they were presented in pairs in each of the six possible pairs of locations (TL + TR, BL + BR, TL + BL, TR + BR, TL + BR, and BL + TR). There was also a condition in which no disc appeared (blank trials).

On a given block of trials, the 10 conditions in which one or two discs appeared were presented five times at each of five intervals following a warning tone. These durations were 500, 600, 700, 800, and 900 msec. Blank trials occurred 25 times. This made a total of 275 trials, which were randomly ordered, per block. Subjects were given four blocks of trials, two in which they responded with the forefinger of the left hand and two in which they responded with the forefinger of the right hand. The order of hands was counterbalanced, with half the subjects receiving the order left, right, right, left, and half right, left, left, right. All subjects received 10 practice

trials, randomly chosen from the total sequence, prior to each block. If they failed to respond within 1 sec of a stimulus, or if they incorrectly responded on a blank trial, the trial was repeated later in the sequence.

### Analysis

Equation 1 represents the prediction of the race model under the assumption of stochastic independence between the two processes. This assumption can be relaxed by noting that the product term,  $P_i P_c$ , must lie between 0 and 1, giving rise to the so-called race inequality (Miller, 1982):

$$P_{ic} \leq P_i + P_c \quad (2)$$

Some authors (Reuter-Lorenz et al., 1995; Miniussi et al., 1998) have documented evidence for enhanced redundancy gain in the split brain in terms of this more conservative equation. We have preferred Equation 1 because it allows redundancy gain to be assessed over the full range of RTs, and not just over the range  $P_i + P_c \leq 1$ . Using the more conservative model does not alter the conclusions of this paper.

Cumulating response probabilities in bins, as described earlier, instead of with reference to real time, provides a common scale on the abscissa, so that the data can be averaged across subjects.

### Acknowledgments

This research was funded by grants from the Marsden Fund of the Royal Society of New Zealand, and from the Human Frontiers Science Project. We thank Giovanni Berlucchi and Bettina Forster for help with the testing in Italy, Matt Roser and Jeff Miller for helpful discussion, and all subjects for their willing participation.

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