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Interhemispheric visuo-motor integration in humans: the effect of redundant targets

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Abstract

We used event-related functional magnetic resonance imaging (fMRI) to investigate the functional locus of response facilitation during parallel visuo-motor processing. In a simple reaction-time task, subjects typically respond faster to two copies of the same stimulus than to a single copy. This facilitation, called the redundant-target effect, can occur at three functional levels: perceptual, 'cognitive' or motor. Normal right handers were studied while performing a simple reaction-time task to unilateral (left or right) and bilateral light flashes. Subjects were instructed to respond with their right index finger. Reaction times were faster to bilateral light flashes than to unilateral ones, even right flashes. Greater fMRI signal for bilateral stimuli compared to unilateral ones was observed in the left precentral and postcentral gyrus, and in the right precentral gyrus. A greater fMRI signal for bilateral and for unilateral left stimuli, compared to unilateral right stimuli, was observed in an area of the right intraparietal sulcus. These results support the hypothesis that the functional locus of response facilitation during parallel visuo-motor processing is premotor.

Introduction

The ability to integrate motor responses to multiple stimuli is a fundamental component of our sensory–motor behaviour. A relevant effect that has been studied for almost a century (Todd, 1912) is the redundant-target effect. When multiple copies of the same stimulus are presented to subjects, in choice, go/no-go and even a simple reaction-time task, reaction times (RT) tend to be faster than RTs to a single copy of the stimulus (Miller, 1982; Miller, 1986). The facilitation has been explained in two ways. According to the statistical facilitation model (Raab, 1962), trials with two stimuli are facilitated because a response can be initiated as soon as either stimulus is detected. According to the coactivation model (Miller, 1982; Miller, 1986), facilitation occurs because the activation produced by the presentation of two stimuli gets multiplied in some way. The concept of coactivation proposed by Miller was abstract and not necessarily linked to neural activity. Recently, however, several studies have assumed that coactivation is equivalent to neural summation (Reuter-Lorenz *et al*., 1995; Corballis, 1998; Miniussi *et al*., 1998; Iacoboni *et al*., 2000; Corballis *et al*., 2002; Corballis, 2002; Roser & Corballis, 2002; Savazzi & Marzi, 2002). In this paper we make the same assumption.

Evidence reported over the years shows that statistical facilitation models are often violated. These violations (henceforth, race model inequality violations, see methods) have been repeatedly reported for divided attention tasks to auditory and visual stimuli (Miller, 1982; Miller, 1986), and go/no-go visual tasks (Mordkoff & Miller, 1993; Mordkoff & Yantis, 1993; Schwarz, 1996). Race model inequality violations have also been observed in simple reaction-time tasks to visual suprathreshold stimuli in split-brain patients (Reuter-Lorenz *et al*., 1995; Corballis, 1998; Iacoboni *et al*., 2000; Corballis *et al*., 2002; Roser & Corballis, 2002). In normal subjects, however, race model inequality violations are more difficult to observe in simple reaction-time tasks (Reuter-Lorenz *et al*., 1995; Corballis, 1998; Corballis *et al*., 2002; Corballis, 2002; Roser & Corballis, 2002). However, even when race model inequality is not violated, especially if very conservative tests are used (Miller, 1982), it cannot be excluded that the facilitation observed is due to neural summation, perhaps a weak one. Moreover, normal individuals show evidence of coactivation if one of the two visual stimuli is below detection threshold (Savazzi & Marzi, 2002), and they also demonstrate considerable intersubject variability. As Corballis (2002; page 431) reports, 'nearly half the subjects show. . .violation of race model at some point in the cumulative distribution. . .'

In principle, the locus of the neural summation can be at a perceptual level, at a central, cognitive or decision level, or at a motor level. The redundant-target effect is typically larger in bimodal tasks (say, an auditory stimulus and a visual one) (Miller, 1982) or cross-dimensional visual tasks (say, colour and shape) (Mordkoff & Yantis, 1993). This suggests that the effect occurs at a stage later than perception (Mordkoff *et al*., 1996). However, a recent electrical scalp recording study of the redundant-target effect has shown that the effect is associated with shorter latency and larger amplitude for early components of the visual event-related potential (ERP) (Miniussi *et al*., 1998). In keeping with these findings, we observed in a previous imaging study that a race model inequality violation in the split brain was associated with activation in extrastriate areas (Iacoboni *et al*., 2000). We interpreted those activations as an index of stronger input to premotor areas, where ultimately coactivation occurs (Iacoboni *et al*., 2000). In fact, some evidence in favour of coactivation occurring at late stages of motor

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programming has also been reported. For instance, it has been shown that intermanual RT differences during bimanual responses get reduced during redundant trials (Diederich & Colonius, 1987). Further, response force tends to be bigger during redundant trials, even though subjects were not instructed to respond more forcefully (Giray & Ulrich, 1993). In tasks requiring stimulus identification, such as go/no-go, however, lateralized readiness potentials (LRP) were not different for single and redundant trials (Mordkoff *et al*., 1996). Moreover, in a stop-signal paradigm requiring subjects to refrain from motor response in some trials, single visual stimuli were more easily inhibited than double visual stimuli and double stop signals were more effective in inhibiting a motor response than single stop signals, leading the authors to suggest a central locus of coactivation prior to late motor stages (Cavina-Pratesi *et al*., 2001). Finally, psychophysical methods applied to single-unit data in primary motor neurons of nonhuman primates performing a simple detection task to single and redundant trials also suggest that late motor processes are not speeded by redundant signals (Miller *et al*., 2001). Any evidence against an early perceptual locus or a late motor locus of coactivation favours the hypothesis of a central, cognitive/decision locus of coactivation which produces the redundant-target effect.

In an attempt to resolve these issues, we used event-related functional magnetic resonance imaging (fMRI), which allows *in vivo* mapping of brain functions with good spatial resolution. So far, the issue of the functional locus of coactivation in the redundant-target effect has been investigated only with electrical scalp recordings, which can provide excellent temporal resolution but coarse spatial resolution. The use of fMRI to measure brain activity while subjects are performing the redundant signals task can illuminate some aspects of the controversy generated by the conflicting results reviewed above. We looked at changes in amplitude of blood oxygenated level-dependent (BOLD) fMRI signal. The prediction is straightforward: brain areas in which coactivation occurs should have bigger BOLD responses to redundant trials than to single trials.

Materials and methods

Subjects

We studied six normal volunteers, four males and two females. They were all right handers, as assessed by a modified version of the Edinburgh Handedness Inventory (Oldfield, 1971), and their mean age was 24.3 ± 2.9 years. All subjects were screened to rule out medication use, a history of neurological or psychiatric disorders, head trauma, substance abuse or other serious medical conditions. No neurological abnormalities were identified by neurological examination performed just before the scanning session. Participants gave informed consent according to the guidelines of the Institutional Review Board at UCLA, which follows the principle of the Declaration of Helsinki.

Imaging

We used a GE 3.0T MRI scanner with an upgrade for echo-planar imaging (EPI) (Advanced NMR Systems, Inc.). A 2-D spin-echo image (TR 4000 ms, TE 40 ms, 256 × 256, 4-mm thick, 1-mm spacing) was acquired in the sagittal plane to screen for the absence of structural abnormalities in the brain and to allow slice prescription of the EPI sequences. A high resolution structural T2-weighted EPI brain volume (spin-echo, TR 4000 ms, TE 54 ms, 128 × 128, 26 slices, 4-mm thick, 1-mm spacing) was initially acquired. This brain volume was coplanar with the functional images subsequently acquired. For each subject, a functional EPI scan (gradient-echo, TR 3000 ms, TE 70 ms, 64 × 64, 21 slices, 4-mm thick, 1-mm spacing) was acquired, for a duration of 3 min and 36 s. The EPI scan consisted of 18 trials of left, right and redundant light flashes (six left-sided, six right-sided, six bilateral), randomly presented. Each trial lasted 12 s, to allow for the return of the BOLD response to baseline (Aguirre *et al*., 1998). Four initial dummy scans were used to allow for the stabilization of the magnetic resonance (MR) signal.

The functional images were aligned with the T2-weighted structural image within each subject using a rigid-body linear registration algorithm (Woods *et al*., 1998a). The images were then registered to a Talairach-compatible (Talairach & Tournoux, 1988) MR atlas (Woods *et al*., 1999) with fifth-order polynomial nonlinear warping (Woods *et al*., 1998b). Data were smoothed using an in-plane Gaussian filter for a final image resolution of 8.7 × 8.7 × 8.6 mm.

Behavioural task

The software MacProbe was used for stimulus presentation and response recording (Hunt, 1994; Zaidel & Iacoboni, 1996). The fMRI unit was equipped with a stimulation and response recording environment controlled by a Macintosh computer system. Visual stimuli were provided with a magnet-compatible Resonance Technology 3-D Visual Stimulation device. To record reaction times we used a magnet-compatible electrostatic pointing device. This device is based upon an ALPS (Alps Electronics, San Jose, CA, USA) 'Glide Point' with multiple response buttons which is connected to a remote stimulus display and response computers via a twisted pair differential line driver which passes through the MR scanner filter panel and then to the Macintosh ADB port.

Subjects saw a fixation cross in the middle of the screen and were presented with stimuli consisting of black flashes on a light grey background. The stimuli subtended 1° of visual angle at 8° of retinal eccentricity to the left or to the right of the vertical meridian and on the horizontal meridian. Stimuli were presented for 50 ms. In each trial there was a random time window of 2000 ms for stimulus presentation. This was done to avoid anticipation of responses in this detection task for which no response selection is required. The random time windows and the variable RT at each trial were compensated by the computer to obtain a fixed total trial time of 12 s. A total of 18 trials (consisting of six unilateral left stimuli, six unilateral right stimuli and six redundant, bilateral stimuli, randomly presented) composed a whole fMRI run. Subjects were instructed to fixate the fixation cross and to respond with a finger key press as soon as they detected the stimulus. Subjects performed a single fMRI run, responding with the right index finger.

RT analysis

Given the small number of trials obtained during the imaging sessions, RT analysis should be considered more descriptive than quantitative. There is an extensive chronometric literature on the paradigm we adopted and on the analysis of RT data (Miller, 1982; Marzi *et al*., 1986; Miller, 1986; Corbetta *et al*., 1990; Marzi *et al*., 1996; Mordkoff *et al*., 1996; Marzi *et al*., 1997; Corballis, 1998; Miniussi *et al*., 1998; Cavina-Pratesi *et al*., 2001; Miller & Low, 2001; Miller *et al*., 2001; Corballis, 2002; Roser & Corballis, 2002). The main purpose of reporting RT data analysis is to show that the two main features often reported in the literature, the redundant-target effect and the violation of race models, were observable in the RT data obtained during the imaging session.

To test for violation of race model inequality, we adopted the approach suggested by Miller (1982). We first rank-ordered RT in each subject for each stimulus type. With the resulting cumulative distribution functions (CDFs) of RT, we then computed an average 6-point CDF for each stimulus type. This was done simply by averaging all the RTs from each subject at each point of the rank order. We then

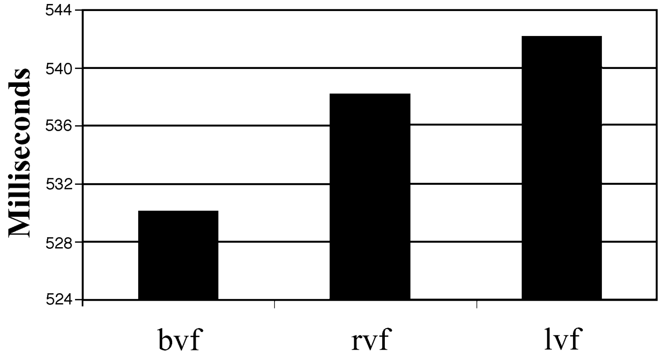

FIG. 1. Mean RT for redundant bilateral trials (bvf), unilateral right visual hemifield trials (rvf) and unilateral left visual hemifield trials (lvf).

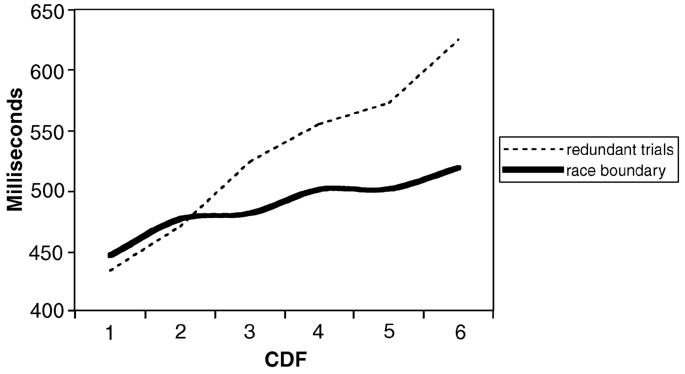

FIG. 2. Cumulative 6-point distribution function (CDF) of redundant trials in comparison with race models boundary. For the fastest RT the CDF of redundant trials is below the boundary of race models, thus violating them.

summed the CDFs for unilateral left and unilateral right trials. The resulting summed CDF was compared to the CDF of the redundant trials (as shown in Fig. 2). When these CDFs are plotted as in Fig. 2, probability models require that the CDF of bilateral trials be everywhere above the summed CDF for unilateral left and unilateral right trials. If the CDF of redundant trials is below the summed CDF of the two unilateral trials at any point of the distribution function, a violation of statistical facilitation or race model inequality occurs (Miller, 1982).

Image statistics

Image statistics was performed with analyses of variance (ANOVAs), allowing to factor out trial-to-trial variability within run as well as intersubject signal variability (Iacoboni *et al.*, 1996; Woods *et al.*, 1996; Iacoboni *et al.*, 1997; Aguirre *et al.*, 1998; Iacoboni *et al.*, 1998; Iacoboni *et al.*, 1999; Iacoboni *et al.*, 2000; Iacoboni *et al.*, 2001; Koski *et al.*, 2002) while modelling the typical haemodynamic response of BOLD fMRI (Aguirre *et al.*, 1998). Factors included in the ANOVAs were subjects ($n = 6$), trial repeats ($n = 6$) and stimulus type (unilateral left, unilateral right, redundant). Significance level was set at $P = 0.001$ uncorrected at each voxel. To avoid false positives, only clusters bigger than 10 significantly activated voxels were considered (Forman *et al.*, 1995).

Results

Mean RT to redundant trials was faster (530 ms) than mean RT to unilateral right stimuli (538 ms) and unilateral left stimuli (542 ms) (Fig. 1). A violation of race model inequality was observed for the fastest RT, a feature that is typically observed when violations of race model inequality occur (Miller, 1982; Miller, 1986) (Fig. 2).

When a contrast between redundant trials and unilateral trials was performed, reliable ($t_{150} = 3.14$, $P = 0.001$ at each voxel) BOLD fMRI signal changes were observed in left precentral and postcentral gyrus, in right precentral gyrus and right intraparietal sulcus (Fig. 3). However, further analyses revealed that BOLD responses at the right intraparietal area were not reliably different for redundant trials vs. unilateral left trials, and that both redundant and unilateral left trials had reliably greater BOLD responses than unilateral right trials.

Discussion

To the best of our knowledge, this is the first report of event-related fMRI data regarding the redundant-target effect in normal subjects. The main question that we addressed here, taking advantage of the spatial resolution of BOLD fMRI, is the locus of the redundant-target effect. As mentioned, previous studies, using different experimental methods, have suggested that the locus of the effect could be visual (Miniussi *et al.*, 1998), central or cognitive/decisional (Cavina-Pratesi *et al.*, 2001; Miller *et al.*, 2001), or motor (Diederich & Colonius, 1987; Giray & Ulrich, 1993). Those studies, however, had used indirect measures for localizing the effect. Most relied on behavioural observations only. Miniussi *et al.* (1998) took advantage of the exquisite temporal resolution of ERP, but had the limiting factor of a relatively poor spatial resolution. With our approach, we observed three regions showing differential responses to the different types of experimental trials: a central left hemisphere region encompassing premotor, primary motor and primary somatosensory cortex, a right premotor region, and a right intraparietal region. We will next discuss the activity profile of these three regions and a unified interpretation of our findings in relation to the available literature.

The activation observed in the right intraparietal sulcus is unlikely to be specific to the redundant-target effect. In fact, no reliable differences in activity were observed between redundant trials and unilateral left trials at that site. Also, the intraparietal area seemed not to respond at all to unilateral right stimuli (see its activity in Fig. 3). This pattern of activity suggests that this region responds to either the presence of visual stimuli in the left visual hemifield or to the integration between a left-sided visual stimulus and a motor response, perhaps only a right-handed one (recall that only right-hand responses were used in this study). It seems that the activity of this region can easily fall within the large category of 'attentional' activity, often associated with the posterior parietal cortex (Andersen *et al.*, 1997). In a previous paper (Iacoboni *et al.*, 2000), we reported fMRI activity associated with race model inequality violation in a right extrastriate area in a patient with callosal agenesis. The area observed in the acallosal patient was much more ventral than the parietal area reported here and, even though one must be careful when comparing the normal and the acallosal brain, we feel that the parietal region observed in this study is too dorsal to be considered functionally comparable to the one we observed in the acallosal subject (Iacoboni *et al.*, 2000).

The activity in the two remaining activated regions is substantially identical, the only real difference between the two regions being their spatial extent, encompassing in one case only the posterior part of the right precentral gyrus and in the other case the central sulcus, precentral and postcentral gyrus in the left hemisphere. The spatial extent and location of the left hemisphere region suggests that this area contains brain activity relevant to premotor, primary motor and primary sensory processing. The specific location of the activation is in the ventral part of the knob of the central sulcus, a location that is compatible with the primary motor hand region (Yousry *et al.*, 1997;

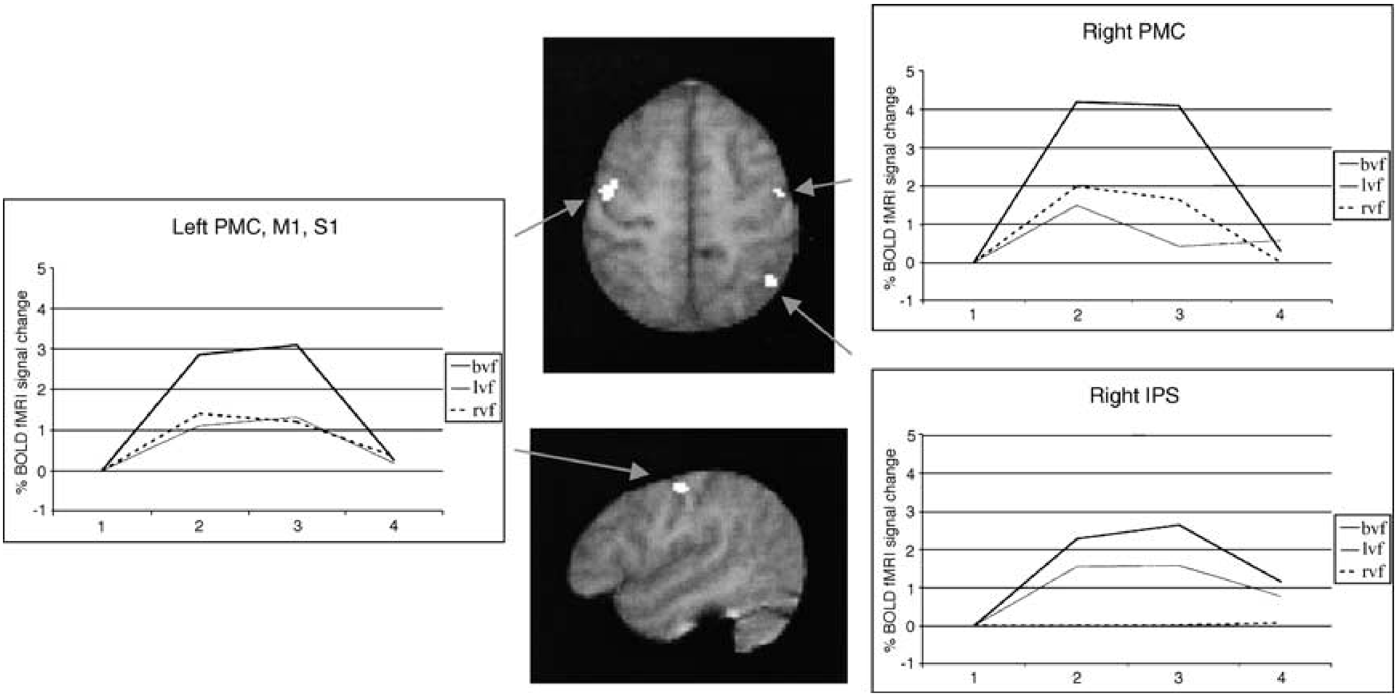

FIG. 3. Areas (PMC, premotor cortex; M1, primary motor cortex; S1, primary somatosensory cortex; IPS, intraparietal sulcus) of differential BOLD responses to stimulus type (redundant trials, bvf; unilateral left, lvf; unilateral right, rvf). The four data points in each graph correspond to the four brain volumes (TR 3000 ms) encompassing the 12-s trials. BOLD activity is expressed as percentage change from the first volume of the trial. Signal changes occur in the second and third volume and go back to baseline in the fourth volume. The sagittal view shows the left hemisphere activation extending into the postcentral gyrus.

Ro *et al*., 1999). The spatial extent and location of the right hemisphere region suggests that only premotor activity is reflected in this activation. The activity profile of both regions shows a much larger response to redundant, bilateral trials than to unilateral ones, whereas there is no difference between left and right unilateral stimuli. This profile seems to genuinely reflect the profile one would expect for areas that are relevant to the redundant signals effect. Thus, our data suggest that the cortical areas relevant to the behavioural effect of redundant signals are the primary motor and somatosensory areas contralateral to the responding hand and also premotor areas bilaterally.

It is not surprising to observe bilateral activation at premotor level even when unilateral motor responses are performed. Motor control at premotor level seems largely bilateral in the primate brain (Passingham, 1993) and our data are consistent with this view. Our data provide a strong support for the hypothesis that the functional locus of the redundant-target effect is at late stages of motor preparation. At first sight, this may be in contrast with some recent interpretation of re-analyses of single-unit data obtained in the macaque primary motor cortex (Miller *et al*., 2001). Those re-analyses have demonstrated that the latency of responses of primary motor neurons is shorter for redundant signals while the time difference from primary motor neural activity to muscle contraction does not change with redundant signals. This has been interpreted as suggesting that the redundant signals effect occurs earlier than in primary motor cortex. Instead, our data show that the redundant signals effect occurs not earlier than in premotor cortex, just one synapse upstream of the primary motor cortex.

The greater activity in primary motor and primary somatosensory cortices may have been produced by more forceful responses to redundant targets (Giray & Ulrich, 1993). It has been shown that there is a high correlation between regional cerebral blood flow in primary motor and somatosensory cortices and force (Dettmers *et al*., 1995). If our subjects involuntarily responded more forcefully to redundant stimuli, a blood flow increase in primary motor and primary somatosensory areas is to be expected. Thus, taken altogether our data seem to suggest that the functional locus of the redundant-target effect is probably premotor. This is somewhat surprising, considering that premotor cortices are known to be important for response selection and stimulus–response association (Passingham, 1993; Iacoboni *et al*., 1996, 1998), two mechanisms which should not play any major role in simple reaction-time tasks. It is possible, however, that the activations we report here may reflect neural activity associated with more basic aspects of response preparation.

The premotor cortices of the two hemispheres are strongly connected by callosal fibres (Zaidel & Iacoboni, 2003). The question that naturally arises here is: what is the role of callosal fibres in the redundant-target effect and in our results? The version of the redundant-target task we used in our study is special: we lateralized the stimuli and the redundant trials are composed of bilateral visual stimuli presented to each hemisphere. Thus, any redundant signals effect observed here must require some level of hemispheric co-operation. It turns out that the version of the task we used has yielded some paradoxical results in the past. Patients with callosal section or callosal agenesis have often shown paradoxically larger facilitation during redundant trials compared to normals (Reuter-Lorenz *et al*., 1995; Corballis, 1998; Iacoboni *et al*., 2000). This has been typically interpreted as reflecting some form of split brain release of subcortical interhemispheric exchange from normal callosal inhibition.

In a previous study, we reported absence of race model inequality violations in patients with anterior callosal section (Iacoboni *et al*., 2000). That previous finding suggests that the bilateral premotor activation observed in the present study in normal subjects may require intact anterior callosal fibres. In the previous study (Iacoboni *et al*., 2000), we also conducted an fMRI experiment in two selected callosal agenesis patients in which we compared two types of redundant trials, one in which stimuli were synchronous and one in which stimuli were asynchronous (Iacoboni *et al*., 2000). The study was performed to test the hypothesis that the transition from a redundant-target effect compatible with race model inequality to a redundant-target effect violating race model inequality was due to long interhemispheric transmission times. The imaging data of our previous study are difficult to compare with the present results because two different populations were used (normals here, acallosals in the previous study) and two different control conditions were employed (unilateral trials here, bilateral redundant asynchronous stimuli in the previous study). What we found was that violation of race model inequality occurring in acallosal patients with long interhemispheric transmission times is associated with BOLD signal increases in extra-striate areas, and not in motor areas. However, we interpreted the extra-striate activations as an index of strong visual input to premotor regions, where coactivation would eventually occur (Iacoboni *et al*., 2000). Taken together, the imaging findings of our previous and current study suggest that coactivation occurs in similar visuo-motor networks in the normal and the split brain, percolating from premotor regions to integrative posterior areas inputting into premotor regions (see Wise *et al*., 1997, for anatomical, physiological and computational considerations compatible with this model). Intact callosal connections may favour late premotor activation whereas cortico-subcortical loops may favour activation in upstream areas.

In conclusion, our data indicate that the functional locus of the redundant signals effect in the normal brain occurs at premotor level bilaterally. These results suggest that response preparation factors are critical for visuo-motor behaviour even in tasks in which motor response difficulty is kept at the lowest possible level. In line with this concept, recent fMRI evidence has suggested that transfer of visuo-motor information in simple reaction-time tasks to lateralized flashes is indeed premotor (Tettamanti *et al*., 2002).

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Abbreviations

BOLD, blood oxygenated level-dependent; CDF, cumulative distribution function; EPI, echo-planar imaging; ERP, event-related potential; fMRI, functional magnetic resonance imaging; LRP, lateralized readiness potential; MR, magnetic resonance; RT, reaction time.

References

Aguirre, G.K., Zarahn, E. & D'Esposito, M. (1998) The variability of human, BOLD hemodynamic responses. *Neuroimage*, **8**, 360–369.

Andersen, R.A., Snyder, L.H., Bradley, D.C. & Xing, J. (1997) Multimodal representation of space in the posterior parietal cortex and its use in planning movements. *Annu. Rev. Neurosci.*, **20**, 303–330.

Cavina-Pratesi, C., Bricolo, E., Prior, M. & Marzi, C.A. (2001) Redundancy gain in the stop-signal paradigm: implications for the locus of coactivation in simple reaction time. *J. Exp. Psychol. Hum. Percept. Perform.*, **27**, 932–941.

Corballis, M.C. (1998) Interhemispheric neural summation in the absence of the corpus callosum. *Brain*, **121**, 1795–1807.

Corballis, M.C. (2002) Hemispheric interactions in simple reaction time. *Neuropsychologia*, **40**, 423–434.

Corballis, M.C., Hamm, J.P., Barnett, K.J. & Corballis, P.M. (2002) Paradoxical interhemispheric summation in the split brain. *J. Cogn. Neurosci.*, **14**, 1151–1157.

Corbetta, M., Marzi, C.A., Tassinari, G. & Aglioti, S. (1990) Effectiveness of different task paradigms in revealing blindsight. *Brain*, **113**, 603–616.

Dettmers, C., Fink, G.R., Lemon, R.N., Stephan, K.M., Passingham, R.E., Silbersweig, D., Holmes, A., Ridding, M.C., Brooks, D.J. & Frackowiak, R.S. (1995) Relation between cerebral activity and force in the motor areas of the human brain. *J. Neurophysiol.*, **74**, 802–815.

Diederich, A. & Colonius, H. (1987) Intersensory facilitation in the motor component? A reaction time analysis. *Psychol. Res.*, **49**, 23–29.

Forman, S.D., Cohen, J.D., Fitzgerald, M., Eddy, W.F., Mintun, M.A. & Noll, D.C. (1995) Improved assessment of significant activation in functional magnetic resonance imaging (fMRI): use of a cluster-size threshold. *Magn. Reson. Med.*, **33**, 636–647.

Giray, M. & Ulrich, R. (1993) Motor coactivation revealed by response force in divided and focused attention. *J. Exp. Psychol. Hum. Percept. Perform.*, **19**, 1278–1291.

Hunt, S.M.J. (1994) Mac Probe: A macintosh-based experimenter's workstation for the cognitive sciences. *Behaviour Research Methods, Instruments and Computers*, **26**, 345–351.

Iacoboni, M., Koski, L.M., Brass, M., Bekkering, H., Woods, R.P., Dubeau, M.C., Mazziotta, J.C. & Rizzolatti, G. (2001) Reafferent copies of imitated actions in the right superior temporal cortex. *Proc. Natl. Acad. Sci. USA*, **98**, 13995–13999.

Iacoboni, M., Ptito, A., Weekes, N.Y. & Zaidel, E. (2000) Parallel visuomotor processing in the split brain: cortico-subcortical interactions. *Brain*, **123**, 759–769.

Iacoboni, M., Woods, R.P., Brass, M., Bekkering, H., Mazziotta, J.C. & Rizzolatti, G. (1999) Cortical mechanisms of human imitation. *Science*, **286**, 2526–2528.

Iacoboni, M., Woods, R.P., Lenzi, G.L. & Mazziotta, J.C. (1997) Merging of oculomotor and somatomotor space coding in the human right precentral gyrus. *Brain*, **120**, 1635–1645.

Iacoboni, M., Woods, R.P. & Mazziotta, J.C. (1996) Brain-behavior relationships: evidence from practice effects in spatial stimulus-response compatibility. *J. Neurophysiol.*, **76**, 321–331.

Iacoboni, M., Woods, R.P. & Mazziotta, J.C. (1998) Bimodal (auditory and visual) left frontoparietal circuitry for sensorimotor integration and sensorimotor learning. *Brain*, **121**, 2135–2143.

Koski, L., Wohlschlager, A., Bekkering, H., Woods, R.P., Dubeau, M.C., Mazziotta, J.C. & Iacoboni, M. (2002) Modulation of motor and premotor activity during imitation of target-directed actions. *Cereb. Cortex*, **12**, 847–855.

Marzi, C.A., Fanini, A., Girelli, M., Ipata, A.E., Miniussi, C., Prior, M. & Smania, N. (1997) Is extinction following parietal damage an interhemispheric disconnection phenomenon?. In Thier, P. & Karnath, H.-O. (eds), *Parietal Lobe Contributions to Orientation in 3D Space*. Springer, Berlin, pp. 431–445.

Marzi, C.A., Smania, N., Martini, M., Gambina, G., Tomelleri, G., Palamara, A., Alessandrini, F. & Prior, M. (1996) Implicit redundant-targets effect in visual extinction. *Neuropsychologia*, **34**, 9–22.

Marzi, C.A., Tassinari, G., Aglioti, S. & Lutzemberger, L. (1986) Spatial summation across the vertical meridian in hemianopics: a test of blindsight. *Neuropsychologia*, **24**, 749–758.

Miller, J. (1982) Divided attention: Evidence for coactivation with redundant signals. *Cogn. Psychol.*, **14**, 247–279.

Miller, J. (1986) Timecourse of coactivation in bimodal divided attention. *Percept. Psychophys.*, **40**, 331–343.

Miller, J.O. & Low, K. (2001) Motor processes in simple, go/no-go, and choice reaction time tasks: a psychophysiological analysis. *J. Exp. Psychol. Hum. Percept. Perform.*, **27**, 266–289.

Miller, J., Ulrich, R. & Lamarre, Y. (2001) Locus of the redundant-signals effect in bimodal divided attention: a neurophysiological analysis. *Percept. Psychophys.*, **63**, 555–562.

Miniussi, C., Girelli, M. & Marzi, C.A. (1998) Neural site of the redundant target effect: electrophysiological evidence. *J. Cogn. Neurosci.*, **10**, 216–230.

Mordkoff, J.T. & Miller, J. (1993) Redundancy gains and coactivation with two different targets: the problem of target preferences and the effects of display frequency. *Percept. Psychophys.*, **53**, 527–535.

Mordkoff, J.T., Miller, J. & Roch, A.C. (1996) Absence of coactivation in the motor component: evidence from psychophysiological measures of target detection. *J. Exp. Psychol. Hum. Percept. Perform.*, **22**, 25–41.

Mordkoff, J.T. & Yantis, S. (1993) Dividing attention between color and shape: evidence of coactivation. *Percept. Psychophys.*, **53**, 357–366.

Oldfield, R.C. (1971) The assessment and analysis of handedness: the Edinburgh inventory. *Neuropsychologia*, **9**, 97–113.

Passingham, R.E. (1993) *The Frontal Lobes and Voluntary Action*. Oxford University Press, New York.

Raab, D.H. (1962) Statistical facilitation of simple reaction times. *Trans. NY Acad. Sci.*, **24**, 574–590.

Reuter-Lorenz, P.A., Nozawa, G., Gazzaniga, M.S. & Hughes, H.C. (1995) Fate of neglected targets: a chronometric analysis of redundant target effects in the bisected brain. *J. Exp. Psychol. Hum. Percep. Perf.*, **21**, 211–230.

Ro, T., Cheifet, S., Ingle, H., Shoup, R. & Rafal, R. (1999) Localization of the human frontal eye fields and motor hand area with transcranial magnetic stimulation and magnetic resonance imaging. *Neuropsychologia*, **37**, 225–231.

Roser, M. & Corballis, M.C. (2002) Interhemispheric neural summation in the split brain with symmetrical and asymmetrical displays. *Neuropsychologia*, **40**, 1300–1312.

Savazzi, S. & Marzi, C.A. (2002) Speeding up reaction time with invisible stimuli. *Curr. Biol.*, **12**, 403–407.

Schwarz, W. (1996) Further tests of the interactive race model of divided attention: The effects of negative bias and varying stimulus – onset asynchronies. *Psychol. Res.*, **58**, 233–245.

Talairach, J. & Tournoux, P. (1988) *Co-Planar Stereotaxic Atlas of the Human Brain*. Thieme, New York.

Tettamanti, M., Paulesu, E., Scifo, P., Maravita, A., Fazio, F., Perani, D. & Marzi, C.A. (2002) Interhemispheric transmission of visuomotor information in humans: fMRI evidence. *J. Neurophysiol.*, **88**, 1051–1058.

Todd, J.W. (1912) *Reaction to Multiple Stimuli*. The Science Press, New York.

Wise, S.P., Boussaoud, D., Johnson, P.B. & Caminiti, R. (1997) Premotor and parietal cortex: Corticocortical connectivity and combinatorial computations. *Annu. Rev. Neurosci.*, **20**, 25–42.

Woods, R.P., Dapretto, M., Sicotte, N.L., Toga, A.W. & Mazziotta, J.C. (1999) Creation and use of a Talairach-compatible atlas for accurate, automated nonlinear intersubject registration and analysis of functional imaging data. *Hum. Brain Mapp.*, **8**, 73–79.

Woods, R.P., Grafton, S.T., Holmes, C.J., Cherry, S.R. & Mazziotta, J.C. (1998a) Automated image registration. I. General methods and intrasubject, intramodality validation. *J. Comput. Assisted Tomogr.*, **22**, 139–152.

Woods, R.P., Grafton, S.T., Watson, J.D.G., Sicotte, N.L. & Mazziotta, J.C. (1998b) Automated image registration. II. Intersubject validation of linear and nonlinear models. *J. Comput. Assisted Tomogr.*, **22**, 153–165.

Woods, R.P., Iacoboni, M., Grafton, S.T. & Mazziotta, J.C. (1996) Improved analysis of functional activation studies involving within-subject replications using a three-way ANOVA model. In Myers, R., Cunningham, V., Bailey, D. & Jones, T. (eds), *Quantification of Brain Function Using PET*. Academic Press, San Diego, CA, pp. 353–358.

Yousry, T.A., Schmid, U.D., Alkadhi, H., Schmidt, D., Peraud, A., Buettner, A. & Winkler, P. (1997) Localization of the motor hand area to a knob on the precentral gyrus. A new landmark. *Brain*, **120**, 141–157.

Zaidel, E. & Iacoboni, M. (1996) Using a computerized system for behavioral laterality experiments. *Brain*, **119**, 2155–2156.

Zaidel, E. & Iacoboni, M. (2003) *The Parallel Brain: the Cognitive Neuroscience of the Corpus Callosum*. MIT Press, Cambridge, MA.