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"The Role of the Corpus Callosum and Bilaterally Distributed Motor Pathways in the Synchronization of Bilateral Upper-Limb Responses to Lateralized Light Stimuli"

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The Role of the Corpus Callosum and Bilaterally Distributed Motor Pathways in the Synchronization of Bilateral Upper-Limb Responses to Lateralized Light Stimuli

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I. How Does the Brain Time Motor Commands for Concurrent Actions of Different Limbs?

The temporal occurrence of different muscle events involved in interlimb motor coordination depends on the timing of the motor commands from the brain as well as the anatomofunctional characteristics of the neural pathways that transmit these commands to the muscles. In one of the simplest tasks involving interlimb motor coordination, a subject is asked to contract a single muscle or muscle group in two limbs simultaneously. Although the contractions in the two limbs are highly correlated in time, as a rule they are never precisely synchronous, even though the subject reports that they are. These deviations from true synchrony do not appear to result from differences in the level of excitability of the motoneuronal pools producing the two actions, nor are they caused by noise or other random or systematic imprecisions in the system. Instead, they reveal that in different situations the brain uses different criteria for assessing the simultaneity of concomitant motor acts.

The relative nature of the judgment of the simultaneity of muscle actions is evident in experiments where subjects are instructed to perform synchronous movements of two different limbs. For example Paillard (1948) and Bard, Paillard, Lajoie, Fleury, Teasdale, Forget & Lamarre (1992) utilized two different experimental paradigms in both of which subjects attempted to achieve subjective simultaneity of muscle actions in two different limbs. In the *reactive* paradigm, subjects were instructed to extend one index finger and elevate the heel of the same side as fast as possible in response to an auditory stimulus. In the *self-paced* paradigm, the subjects performed these movements spontaneously, in the absence of any external triggers. The reaction times (RT) of the two concurrent responses in the reactive condition were indistinguishable from those of the two responses when tested alone (i.e., the RT of the finger response was systematically shorter than that of the heel response). By contrast, in the self-paced condition the elevation of the heel systematically preceded the extension of the finger. Evidently, in the reactive condition the two motor commands were released simultaneously but the difference in length between the efferent pathways caused the command for the finger response to reach its muscle effectors sooner than did the command for the heel response. By contrast, in the self-paced condition the two motor commands were shifted in time as if the brain took the different lengths of efferent and afferent pathways into account and strived to obtain a simultaneous return of reafferent signals from the two moving limbs. In accord with this interpretation, a polineuropathy patient with a somatic sensory deafferentation was found to display a precession of the short-pathway finger response

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over the long-pathway heel response in both reactive and self-paced conditions (Bard *et al.*, 1992). Normal subjects always claimed that the two movements were synchronous independent of the reactive or self-paced mode of performance, although the movements were in fact asynchronous in both conditions. In the reactive condition subjective synchrony was probably predicated on the effective synchronization of the two motor commands by the external trigger, while in the self-paced condition it seemed to be engendered by the expectation of synchronous peripheral consequences from two properly desynchronized motor commands.

II. Lateral Reaction Time Differences in Simple Visuomotor RT

The lengths of peripheral sensory pathways and the conduction velocities of afferent fibers have long been known to play an important role in determining the temporal aspects of sensation and perception (e.g., Piéron & Jones, 1959). The results of Paillard (1948) and Bard *et al.* (1992), illustrated above, indicate that the anatomofunctional properties of peripheral neural pathways, efferent as well as afferent, are also relevant to the timing of motor commands intended to produce synchronous movements. It would appear that the time course of sensory and motor events must similarly be affected by the organization of the underlying central neural pathways and the speed with which they transfer information. In 1912, Poffenberger applied chronometric analysis to the dissection of the central neural pathways subserving the execution of a fast manual or digital movement (such as pressing a key) in reaction to a simple visual stimulus, a light flash presented in the right or left hemifield. Because of the organization of the optic pathways, a light flash presented in such a manner is projected to the visual cortex of the opposite hemisphere. The motor reaction of each hand is under the control of the contralateral hemisphere because of the crossing of the major motor pathways. Uncrossed reactions (i.e., reactions of each hand to stimuli in the ipsilateral hemifield) can thus be integrated within a hemisphere, whereas crossed reactions (i.e., reactions of each hand to contralateral hemifield stimuli) require an interaction between the hemisphere receiving the visual stimulus and that emitting the response, probably through the corpus callosum. On this basis, Poffenberger (1912) argued that the RT of crossed responses should be longer than the RT of uncrossed responses, and that the crossed–uncrossed time difference (CUD) should correspond to the extra time needed for interhemispheric communication. He did find a CUD of a few milliseconds in the expected direction, and his finding has been repeatedly confirmed by modern studies, which have demonstrated CUDs of 2–3 msec, a difference that is accounted for by the conduction time along the largest fibers of the corpus callosum (Tassinari, Morelli & Berlucchi, 1983; Levy & Wagner, 1984; St. John, Shields & Timney, 1987; Vallar, Sterzi & Basso, 1988; Milner, Jeeves, Silver, Lines & Wilson, 1985; Clarke & Zaidel, 1989; Saron & Davidson, 1989; Aglioti, Dall'Agnola, Girelli & Marzi, 1991; Marzi, Bisiacchi & Nicoletti, 1991; Di Stefano, Sauerwein & Lassonde, 1992; for earlier studies see the review by Bashore, 1981). The direct relation of the CUD to interhemispheric transfer is supported by findings of abnormal, exceedingly long CUDs in subjects with defective interhemispheric comnication, such as subjects with callosal agenesis (Jeeves, 1969; Reynolds & Jeeves, 1974; Milner, 1982; Milner *et al.*, 1985; Di Stefano *et al.*, 1992; Aglioti, Berlucchi, Pallini, Rossi & Tassinari, 1993) and patients with complete callosotomy (Sergent & Myers, 1985; Clarke & Zaidel, 1989; Aglioti *et al.*, 1993). In these patients, intact central channels for interhemispheric communication at subcortical levels suffice for ensuring the cross-midline interactions needed for performing crossed responses. Yet transfer of information by these acallosal pathways appears to be at least ten times slower than normal interhemispheric transfer via the corpus callosum (Aglioti *et al.*, 1993).

The brief nature of the CUDs in normal control subjects is not a simple manifestation of spatial stimulus–response compatibility. Spatial stimulus–response compatibility consists of a speed advantage for a response present when stimulus and response are matched for side. Spatial compatibility effects occur in choice RT tasks, while CUDs are demonstrated by simple RT paradigms. Previous studies in normals have clearly differentiated CUDs, which depend crucially on the specific anatomic relations between visual hemifields, cerebral hemispheres, and the responding hand (e.g., Berlucchi, Crea, Di Stefano & Tassinari, 1977), from spatial compatibility effects, which arise from the match or mismatch between the code for the location of the stimulus and the code for the location of the response (e.g., Umiltà & Nicoletti, 1990). The long CUDs of subjects with a defect of the corpus callosum, whether congenital (Milner *et al.*, 1985) or acquired (Aglioti *et al.*, 1993), have also been convincingly distinguished from spatial compatibility effects. As an example, Figure 1 shows that the CUD of a patient with a complete section of the corpus callosum was unaffected by the spatial relations between the position of the visual stimulus and that of the responding hand. The right hand was faster than the left in responding to right-hemifield stimuli, and the left hand was faster than the right in responding to left-hemifield stimuli, regardless of whether either hand worked in the right or left hemispace. CUDs were tested on two blocks of 30 trials in which the patient pressed the right key with the right thumb and the left key with the left thumb; and in two other blocks,

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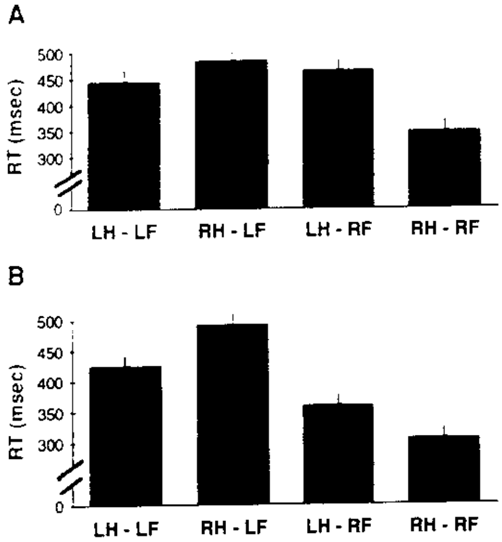

FIGURE 1 Crossed–uncrossed differences in a callosotomized subject as a function of hand position. The figure shows mean RTs (plus S.E.) of each hand (RH, right hand; LH, left hand) in each visual hemifield (LF, left hemifield; RF, right hemifield) in the normal (A) and inverted (B) hand positions. An analysis of variance having hemifield, hand, and hand position as main factors showed the hemifield/hand interaction to be highly significant ($p < .01$). The three-way interaction was completely insignificant, demonstrating that hand position did not affect the hemifield/hand interaction. The advantage of uncrossed RTs over crossed RTs was significant and similar in both hemifields and in both conditions, with overall CUDs of 78 msec in the normal hand-position condition, and 60 msec in the inverted hand-position condition. See Aglioti *et al.* (1993) for further details.

again of 30 trials, in which the patient held the responding arm across the midline in order to press the right key with the left thumb and the left key with the right thumb, so that uncrossed responses were performed with the hand in the hemispace contralateral to the visual stimulus, and crossed responses were performed with the hand in the hemispace ipsilateral to the visual stimulus. In each block of both conditions (the normal hand-position condition and the inverted hand-position condition), the location of the visual stimulus (a gallium phosphide green flash with a 5-msec duration and an intensity of about 1000 μcd on a background of .15 cd/m^2) varied randomly between 10° to the right and 10° to the left of fixation, with the constraint that each block included 15 right and 15 left stimuli. In each condition the trials of one block were performed with the right hand and those of the other block were performed with the left hand. The order of presentation of the four blocks was decided on a random basis according to a Latin square design.

In Figure 2, data are shown from an experiment on the same callosotomized subject as in Figure 1, in which reaction times were compared with the corresponding latencies of activation of the prime movers, that is, the muscles primarily involved in the performance of the response, as indicated by their electromyographic (EMG) activities. Behavioral reaction time can be divided into a premotor time, that is, the lag between the stimulus and the first EMG activation of the prime movers, and a motor time, or the differential between reaction time and premotor time. Only premotor time can serve as a reliable direct indicator of the temporal course of central neural processes, since motor time is mainly determined by the speed in attaining the force value necessary for overcoming the inertial load of the response device. Premotor times of crossed and uncrossed responses were assessed by recording the EMG with surface silver electrodes attached to the skin overlying the thenar muscles of the responding hand. Concurrent measures of premotor times and reaction times of crossed and uncrossed responses allow one to evaluate the relative contributions of central and peripheral factors to the crossed–uncrossed difference in reaction time. Figure 2 shows that the long CUD was by no means caused by a slower development of force on crossed as compared to uncrossed responses,

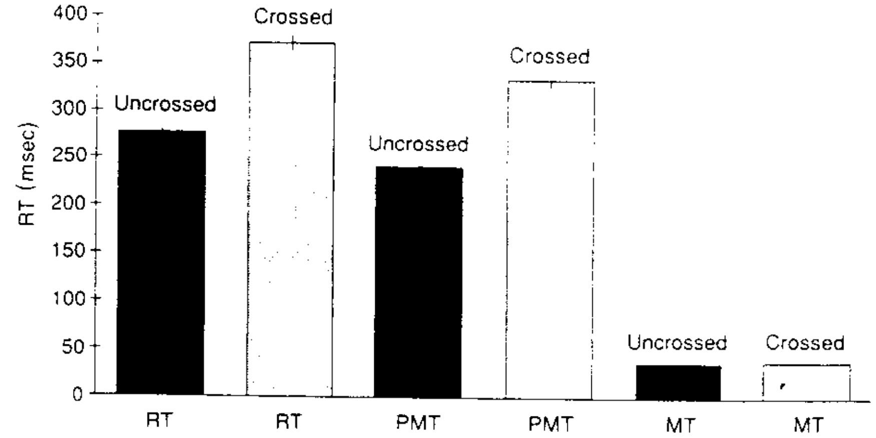

FIGURE 2 Crossed–uncrossed differences in reaction time, premotor time, and motor time. The figure shows the means (plus S.E.) of reaction times (RT), premotor times (PMT), and motor times (MT) of uncrossed responses, that is, responses made with the hand attached to the side of the body ipsilateral to the visual stimulus, and crossed responses, that is, responses made with the hand attached to the side of the body opposite the visual stimulus. Crossed–uncrossed differences in RT are entirely accounted for by crossed–uncrossed differences in PMT, since MTs are equal for the two classes of response. Crossed–uncrossed differences in RT and PMT are significant at the $p < .01$ level. Each column represents 45 data points (see Aglioti *et al.*, 1993).

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since EMG recordings from prime movers demonstrated that CUDs derived from RTs were entirely accounted for by crossed–uncrossed differences between premotor times, that is, prior to the activation of motoneurons (Aglioti *et al.*, 1993).

III. Crossed–Uncrossed Differences in Bilateral Responses to Lateralized Light Stimuli

If the CUD is due to a difference in length between the pathways subserving crossed and uncrossed responses, then it should also be found when subjects respond bilaterally to a lateralized flash. Significant CUDs on bimanual responses to lateralized flash are indeed exhibited by normal control subjects (Jeeves, 1969; Di Stefano, Morelli, Marzi & Berlucchi, 1980) as well as by callosal agenetics (Jeeves, 1969; Reynolds & Jeeves, 1974; Milner *et al.*, 1985). Recently we have replicated this finding also in a patient with a complete section of the corpus callosum (Aglioti *et al.*,1993).

Table I summarizes the results of these studies and allows a comparison between CUDs on unimanual and bimanual tasks in different groups of subjects. It is clear from the table that (1) all groups displayed positive CUDs in both unimanual and bimanual responding conditions; (2) CUDs of subjects lacking a corpus callosum were much longer than those of normals in either condition; and (3) all groups showed smaller CUDs under bimanual than under unimanual responding conditions. An additional finding was a definite tendency to synchronization of motor output in the bimanual task in all groups, as attested by the occurrence of clear-cut correlations between crossed and uncrossed RTs when these were compared on a trial-by-trial basis (Di Stefano *et al.*, 1980; Milner, 1982; Milner *et al.*, 1985; Aglioti *et al.*, 1993). Figure 3 gives examples of these correlations in a callosotomized patient from the study of Aglioti *et al.* (1993). It is understood that given the irreducibility of the CUD in normals and acallosals alike, these strong correlations occur in spite of the absence of a true bilateral simultaneity of crossed and uncrossed responses. It should also be clear that the above crossed–uncrossed differences and correlations are quite distinct from right–left differences and correlations, which may be observed in bilateral symmetrical movements (e.g., Hongo, Nakamura, Narabayashi & Oshima, 1976). Samples of crossed and uncrossed RTs obviously include RTs for each hand and each hemifield in the appropriate combinations. Therefore, their distributions and central tendencies are unaffected by systematic differences between the right and left hands (or the right and left hemifields), as these are bound to cancel each other in the combinations.

TABLE I **Crossed–Uncrossed Differences (CUDs) in Different Groups of Subjects under Unimanual and Bimanual Responding Conditions**

		CUD (msec)	
Reference	**Subject(s)**	**Unimanual**	**Bimanual**
Jeeves, 1969[a]	10 Normal adults	2.82	1.68
Reynolds & Jeeves, 1974[a]	1 Acallosal[b] girl	30.36	12.95
Di Stefano *et al.*, 1980[c]	12 Normal adults	2.20	.80
Milner *et al.*, 1985[c]	1 Acallosal[b] boy	12.60	8.00
Aglioti *et al.*, 1993[c]	Callosotomized adult M. E.[d]	69.60	37.90
Aglioti *et al.*, 1993[c]	Acallosal[b] adult R. B.[e]	18.05	11.70
Aglioti *et al.*, 1993[c]	Acallosal[b] adult P. M.[e]	25.45	14.40

[a] Averaged across temporal and nasal hemiretinae in monocular stimulation.

[b] Callosal agenesis.

[c] Binocular stimulation.

[d] Male subject M. E., born in 1970, was submitted to a complete section of the corpus callosum at the Neurosurgical Institute of the Catholic University in Rome (Prof. G. F. Rossi). Callosotomy was performed in two stages (February and June 1989) in an attempt to control a form of post-traumatic epilepsy with complex partial seizures and secondary generalization which had proved totally resistent to pharmacological therapy as well as to a removal of a focus in the right prefrontal cortex. Callosotomy has resulted in a marked favorable change in both severity and frequency of the seizures. Pharmacological treatment with Phenobarbital and Phenytoin has been continued throughout the postoperative period. At the times of testing for RT (April and October 1990, June and December 1991), standard clinical examinations revealed a stationary condition with no neurological deficits except for a severe left-hand ideomotor dyspraxia on verbal command (but not on imitation), a left-hand anomia and alexia in the left hemifield. The completeness of the callosal section and the integrity of the anterior commissure have been confirmed by magnetic resonance imaging.

[e] R. B. and P. M. are two young men, aged 16 and 31 years, respectively, who have been diagnosed by MRI as congenitally lacking the corpus callosum. They are free from major neurological symptoms and appear to have normal intelligence, as indicated by their current respective performances in a technical school and a mechanical shop.

The finding of significant CUDs and crossed–uncrossed correlations in normals as well as in acallosals emphasizes the importance of the corpus callosum in bilateral motor control. Although the corpus callosum may be assumed to play a coordinating role in the synchronization of motor outputs from different hemispheres, the balance of evidence so far has instead suggested a primarily desynchronizing and differentiating callosal action in complex bimanual tasks. Thus, split-brain patients and callosal agenetics have been reported to suffer from a specific disability to suppress synchrony and symmetry of bimanual movements in dual tasks that call for differentiated actions of the two hands (Preilowski, 1972; Jeeves, Silver & Jacobson 1988; Tuller & Kelso, 1989). To the extent that strong crossed–uncrossed correlations in simple reactions to lateralized flashes occur in normal and acallosal subjects alike, at first sight the above RT findings also seem to dismiss a participation of the corpus callosum in the synchronization of concurrent symmetrical movements of the hands in a simple visuomotor task. However, owing to the different CUD magnitudes, bimanual performance comes much closer to synchrony in normals than in acallosals, justifying the assumption of a normal callosal contribution to synchronization of bimanual responses to a lateralized visual input. Since the absence of the corpus callosum leads to an increased difference in length between the pathways for crossed and uncrossed reactions, bilateral asynchrony is bound to be greater in acallosals than in normals.

In a sense, a subject performing conjoint crossed and uncrossed manual responses to a flash presented in the right or left hemifield is comparable to one making concurrent responses with the index finger and the heel of one side to a nonlateralized auditory stimulus, as in the experiments by Paillard (1948) and Bard *et al.* (1992). In both cases one of the concurrent responses is subserved by a relatively short pathway (respectively, the intrahemispheric pathway for the visuomotor response and the pathway for the finger response) and the other is subserved by a relatively long pathway (respectively, the interhemispheric pathway for the visuomotor response and the pathway for the heel response). Paillard (1948) and Bard *et al.* (1992) showed that the precession of the finger response on the heel response in the double-response task coincided with the difference in RT between the two responses when tested independently. If, for present purposes, their situation is similar to that of the bimanual visuomotor task, then the latter task should yield a CUD comparable to that found on unimanual responding. Acallosal subjects compare with normal controls in showing reduced CUDs under the bimanual relative to the unimanual responding condition. At variance with the experiments of Paillard (1948) and Bard et al. (*1992*), the difference between crossed and uncrossed RTs is smaller upon bimanual than upon unimanual responding. Theoretically, this CUD reduction may result from either an increased speed of the slower (crossed) responses, or a decreased speed of the faster (uncrossed) responses in comparison to the unimanual task. In patients with hemiparesis or hemianesthesia from lateralized brain damage, the advantage of the RT of the normal hand over the RT of the affected hand diminishes on bilateral compared to unilateral responding: the disadvantaged response is speeded up selectively in the bimanual task, as if its execution were aided in some way by the concurrent motor command from the undamaged hemisphere to the normal side (Jung & Dietz, 1975; Jeannerod, 1988, p. 82). By contrast, some of the data from our callosotomized patient suggest that the CUD reduction on bimanual compared to unimanual responses was obtained by slowing down

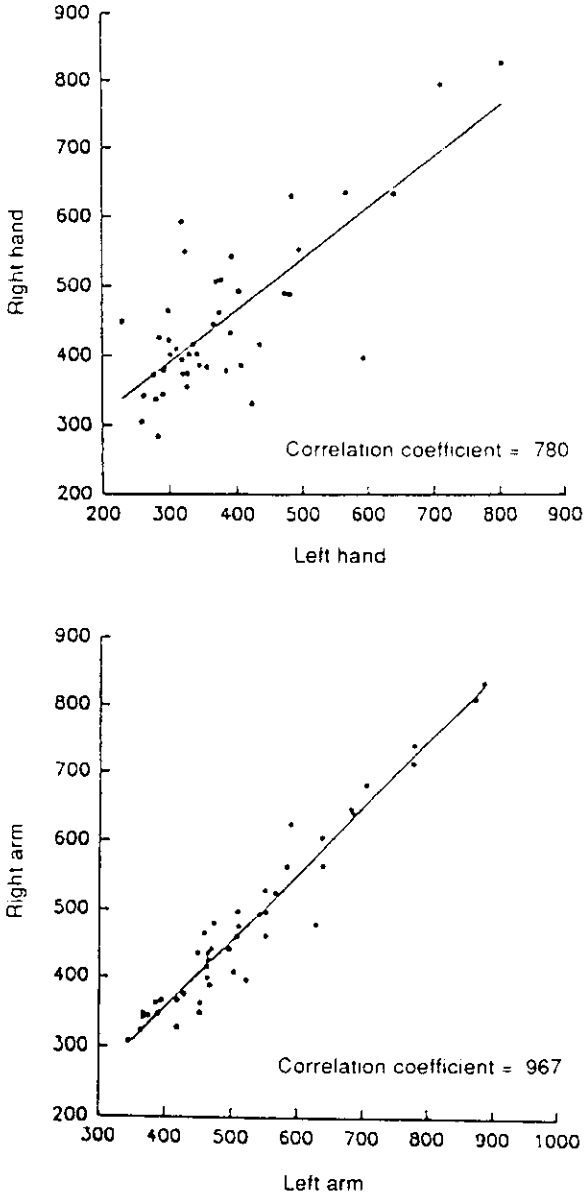
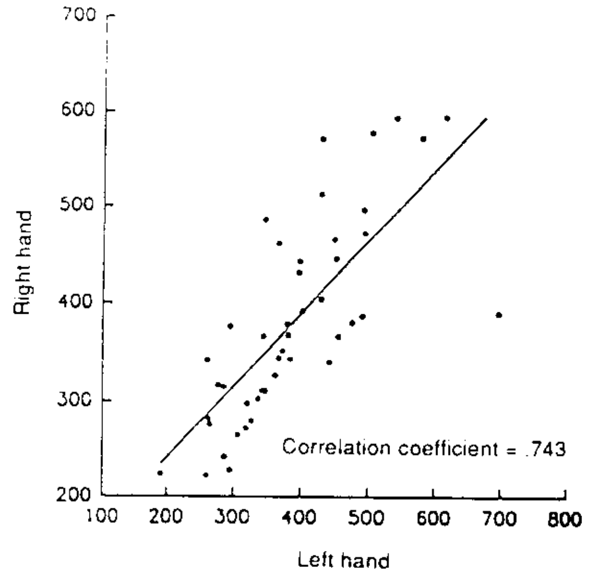
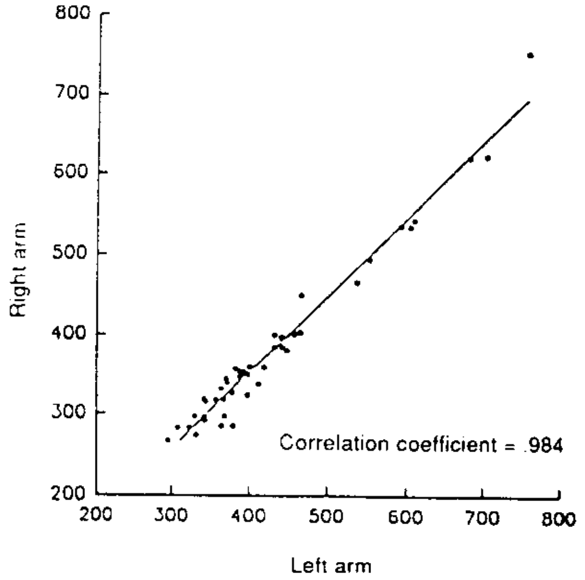


FIGURE 3 Side-to-side correlations in bilateral distal and proximal responses after callosotomy. The figure shows scattergrams and regression lines for bilateral distal (key pressing) and proximal (lever pulling) responses (in msec) upon left and right hemifield stimulation (left graphs and right graphs, respectively) in a callosotomized subject (see Aglioti *et al.*, 1993). Each diagram is based on 45 reaction times. It is clear that in the subject, distal responses are less correlated than proximal responses. However the corre-





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lation coefficients for the distal responses (.780 for the left hemifield and .743 for the right hemifield) fall just above the lower limit of the normal range (.730–.960) reported by Di Stefano *et al.* (1980). The subject's correlation coefficients for the proximal response (.967 for the left hemifield and .984 for the right hemifield) are fully comparable to the mean (.970) of the corresponding coefficients reported by Di Stefano *et al.* (1980) for normal controls (range .950–.980).

uncrossed responses relative to crossed responses. This finding is akin to an effect seen in normal subjects on dual tasks, where the two hands perform highly differentiated actions characterized by different degrees of difficulty. Usually the easy performance with one hand is slowed down so that its motor time comes to coincide with that of the difficult performance with the other hand (Kelso, Putnam & Goodman, 1983).

The responses studied in our simple bilateral tasks are likely to be emitted almost in a reflexlike fashion via relatively fixed and straightforward connections between visual and motor centers. Thus a perfect match between the short-pathway RT and the long-pathway RT cannot be expected on structural considerations alone, particularly where the absence of the corpus callosum increases the difference in length between the pathways. However, the speed of information transfer along these different pathways may be controlled by a superordinate center so as to effect a temporal coordination of the motor outputs of the two hemispheres. Experiments employing different paradigms from the present one have supported the notion that acallosal subjects possess mechanisms for gross synchronization and equalization of bilateral symmetrical movements (Tuller & Kelso, 1989) or for simple postural adjustments of one hand in anticipation of a movement of the other hand (Viallet, Massion, Massarino & Khalil, 1992). Alternatively, an interfering crosstalk between the motor systems controlling the two hands (e.g., Marteniuk, MacKenzie & Baba, 1984), rather than a truly coordinating action, may be responsible for the slowing down of the fastest response upon bilateral responding, and thus for the tendency to bimanual synchronization. There is no decisive argument in favor of one or the other assumption, both of which, however, concur in implying that either the coordinating or the interfering action must be able to operate between the hemispheres through both callosal and extracallosal pathways.

IV. Responses to Lateralized Flash with Movements Controlled by Bilaterally Distributed Motor Systems

We have seen that an interhemispheric transfer is necessary for responding with one hand to a stimulus in the contralateral visual field. A bilateral manual response to a lateralized flash engages motor systems in both hemispheres because moving each hand calls for a command from the appropriate hemisphere. By contrast, other upper-limb movements can be directly initiated by either hemisphere through bilaterally distributed motor pathways. Bilaterally distributed motor systems originating from each hemisphere are indeed available for the activation of axial and proximal limb muscles involved in global body movements, general postural adjustments, and integrated synergistic limb–body movements. Their existence has been demonstrated anatomically and physiologically in nonhuman primates (Kuypers, 1987; 1989) and confirmed by clinical and experimental evidence in humans (e.g., Freund, 1987; Colebatch & Gandevia, 1989; Müller, Kunesch, Binkofski & Freund, 1991; Colebatch, Deiber, Passingham, Friston & Frackowiak, 1991; Benecke, Meyer & Freund, 1991). The chief exponent of unilaterally distributed motor pathways is the crossed component of the corticospinal tract, while that of the bilaterally distributed motor systems is the cortico-reticulo-spinal tract.

Thus, it is theoretically possible for a visual input channeled into a single hemisphere to directly initiate and guide axial and proximal limb movements on both sides of the body, and CUDs may be expected to be absent when crossed as well as uncrossed visuomotor responses can be initiated by the hemisphere receiving the flash. Di Stefano *et al.* (1980) compared in normal subjects the CUD on a distal response, consisting of a keypress by a flexion of the thumb, with the CUD on a proximal response, consisting of a leverpull by a flexion of the forearm. They found indistinguishable significant CUDs for both types of response, but only when the responses were made unilaterally. A comparable result was reported by Milner, Miln & MacKenzie (1989), who found no differences in the CUD between a finger–thumb opposition response and an index lifting response presumably involving a movement of the whole hand. However, Di Stefano *et al.* (1980) described an annulment of the CUD on proximal responses (but not on distal responses) when such responses were executed bilaterally in reaction to the lateralized flash. Apparently, unilateral crossed responses to the flash, both distal and proximal, are elicited from the contralateral motor cortex and thus require an interhemispheric integration. On the contrary, bilateral proximal responses to a lateralized flash are actuated by a bilaterally distributed motor system, which ensures an approximate simultaneity of crossed and uncrossed reactions without the aid of interhemispheric integration. Quite recently we have found a similar absence of a CUD on an axial response consisting of an elevation of the shoulder, but in both unilateral and bilateral responding conditions (Tassinari, Berlucchi & Aglioti, in preparation). This finding suggests the possibility that responses of each shoulder can be effectively controlled by either the ipsilateral or contralateral hemisphere, in agreement with the pattern of motor cortex activation recently found during unilateral shoulder movements (Colebatch *et al.*, 1991).

The overall pattern of CUDs in normal subjects evidenced by the studies of Di Stefano *et al.* (1980), Milner *et al.* (1989), and Tassinari *et al.* (in preparation) allows a clear-cut distinction between crossed responses that presumably utilize interhemispheric transfer from those

TABLE II Presence or Absence of the CUD According to the Musculature and the Type of Task Involved

	Musculature involved		
	Distal	**Proximal**	**Axial**
Unilateral task	Presence	Presence	Absence
Bilateral task	Presence	Absence	Absence

that presumably do not (see Table II). The first set of responses includes unilateral and bilateral distal responses and unilateral proximal responses of the upper limb, all associated with significant CUDs, reflecting dependence on interhemispheric transfer. The second set includes bilateral proximal responses and unilateral and bilateral axial responses of the upper limb, all associated with null CUDs, reflecting independence from interhemispheric transfer. Logically, this distinction leads one to predict that impairment of interhemispheric transfer by callosal defects should alter the CUDs associated with the first set of responses, but not those associated with the second set. The CUD pattern that we found in a completely callosotomized subject fit this prediction very well (Aglioti *et al.*, 1993). This subject showed CUDs on unilateral and bilateral distal responses and on unilateral proximal responses that were at least an order of magnitude greater than the typical 2–3 msec corresponding to CUDs of normal subjects. In the conditions that yield null CUDs in normal subjects, that is, bilateral proximal responses and both unilateral and bilateral axial responses, this subject exhibited insignificant or null CUDs (Figure 4).

Bilateral axial and proximal upper-limb responses to lateralized flashes are highly correlated. In addition, the correlation for proximal responses is substantially higher than that for distal responses,in normal subjects as well as in the acallosal subject (see Figure 3). These responses are also synchronous inasmuch as the crossed RT does not differ from the uncrossed RT, and again this is as true in the acallosal as in the normal control subjects. This difference with the systematic asynchrony of bilateral distal responses is best explained by assuming that such responses always require the concurrent activation of two motor commands, one from each hemisphere, whereas bilateral proximal and axial response can be issued after one motor command from a single hemisphere. An additional assumption is that unilateral proximal responses of the upper limb are effected through a crossed pathway, whereas the same responses, when made bilaterally, engage a different, bilaterally distributed motor system, which ensures a yoked movement of the two sides. Experimental evidence concerning facial

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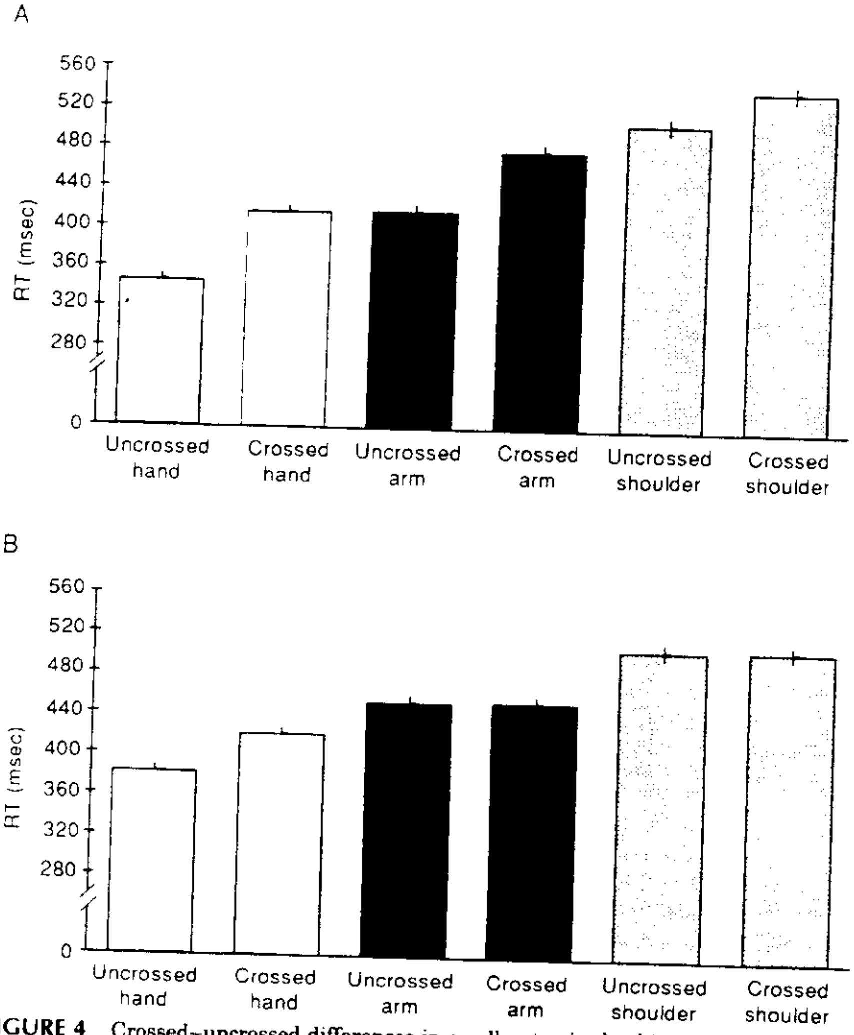

FIGURE 4 Crossed–uncrossed differences in a callosotomized subject as a function of responding effector and unilateral (A) or bilateral (B) responding condition. The figure gives mean reaction times (plus S.E.) for crossed and uncrossed distal (hand) responses, proximal (arm) responses, and axial (shoulder) responses in both the unilateral and the bilateral responding condition. Crossed and uncrossed responses are as defined in Figure 2. Uncrossed reaction times (RT) are significantly shorter ($p < .01$) than crossed RTs on unilateral and bilateral distal responses and on unilateral proximal responses; crossed–uncrossed differences on the remaining responses, including the unilateral axial (shoulder) response, are statistically insignificant. Each column represents 90 reaction times.

motility supports the hypothesis that unilateral components of a bilateral response can be produced by neural systems different, at least in part, from those mediating the same movements when made unilaterally. For example, Gazzaniga and Smylie (1990) found that in the generation of posed smiling by the left hemisphere of commissurotomy patients, the right side of the mouth began to move 90–180 msec before the left side, a facial CUD comparable in both kind and degree with those observed with hand and arm responses in our callosotomized subject. However, the same comissurotomy patients did not display any facial asymmetry during spontaneous smiling, suggesting the operation of a different bilaterally synchronizing motor system. Since the corpus callosum had been cut, bilateral synchronization was obviously achieved independent of fast interhemispheric coordination.

V. Summary and Conclusions

Speeded bilateral symmetrical responses to visual inputs restricted to one hemisphere can never be perfectly synchronous. This appears to be due to the difference in length between the neural pathways mediating the responses on the two sides. When the two responses are emitted by different hemispheres, as it occurs with distal hand movements, there is an irreducible advantage in speed for the response emitted by the hemisphere that receives the visual stimulus. However, this advantage is minimized by the corpus callosum, which allows an efficient interhemispheric communication for the fast integration of the disadvantaged response. This syncronizing callosal influence is inferred from the increased asynchrony of bilateral hand responses, which occurs in the absence of the corpus callosum, whether congenital or acquired. However, the persistence of strong temporal correlations between bilateral hand responses to lateralized visual stimuli in acallosal patients suggests a nonnegligible contribution of extracallosal mechanisms to the temporal coordination of the motor outputs from the two hemispheres. These extracallosal mechanisms for bilateral temporal coordination of hand responses are not yet understood. More information is available as to the mechanisms that ensure the bilateral synchronization of responses effected with axial and proximal arm muscles. Each hemisphere can control these responses on both sides of the body, so that the synchronization between the two sides is made possible by the common origin of the motor commands and by the bilateral distribution of the pathways transmitting them. In this case, bilateral synchronization is totally independent from the corpus callosum.

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