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RESEARCH ARTICLE

Yuko Taniguchi · Borís Burle · Franck Vidal
Michel Bonnet

Deficit in motor cortical activity for simultaneous bimanual responses

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Abstract Reaction time (RT) is known to be longer for simultaneous bimanual responses than for unimanual ones. This phenomenon is called “bilateral deficit”. To identify the mechanisms subserving the bilateral deficit, brain electrical activity was examined, with a source derivation method, in 12 right-handed subjects, during the preparation and execution periods of a RT task. The responses were either unilateral or bilateral index finger flexion, performed either in a simple RT condition, with 20% catch trials, or in a choice RT condition. A deficit was observed in RT for the bilateral response for the right-index finger movement. In cerebral electrical activities, no evidence of a correlate of a bilateral deficit was found during the preparatory period. Conversely, during the execution period, an EEG correlate of the bilateral deficit was found. For the right hand, the activation of the sensorimotor area directly involved in the voluntary control was weaker for bilateral than for unilateral contralateral responses. The reasons for such a bilateral command weakness are discussed in the context of our RT task. First, the constraint of synchronisation included in the bilateral response might require an interhemispheric information transmission that resulted in a braking effect. Second, given that an ipsilateral inhibition is present in case of choice between the two hands of one particular unimanual response, and given that this ipsilateral inhibition is also present in case of simple unimanual trials, we hypothesise that a mutual transcallosal inhibitory effect also persists in the bilateral response.

B. Burle · F. Vidal · M. Bonnet (✉)
Centre de Recherche en Neurosciences Cognitives,
C.N.R.S. – C.R.N.C. 31 Chemin Joseph Aiguier,
13402 Marseilles Cedex 20, France
e-mail: bonnet@lnf.cnrs-mrs.fr
Fax: +33-491-774969

Y. Taniguchi
Department of Physical Education, International Budo University,
841 Shinkan, Katsuura, Chiba 299-5295, Japan

F. Vidal
Institut de Médecine Navale du Service de Santé des Armées,
BP 610, 83800 Toulon Naval, France

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Introduction

Maximal voluntary strength of simultaneous bilateral exertion has been found to be smaller than the sum of the unilateral exertions (Henry and Smith 1961; Howard and Enoka 1991; Koh et al. 1993; Oda and Moritani 1995; Ohtsuki 1981b, 1983; Rube and Secher 1990; Schantz et al. 1989; Taniguchi 1997, 1998; Vandervoort et al. 1984). This phenomenon is called “bilateral deficit”. In addition, when simultaneous bilateral movements are produced in reaction time (RT) tasks, RTs are longer than in unilateral conditions (Di Stefano et al. 1980; Kerr et al. 1963; Ohtsuki 1981a; Steenbergen et al. 1996; Taniguchi 1999).

Ohtsuki (1983, 1994) considered that there may be two possible mechanisms, among many, subserving these bilateral deficits: division of attention and interhemispheric inhibition. The hypothesis of a division of attention assumes that when a bilateral simultaneous task is performed as a combination of two independent unilateral tasks, a limited amount of attention is distributed to each task. Thus, the attention allocated to each movement should decrease and, as a result, force and speed (integral of force divided by mass) would decrease. However, Howard and Enoka (1991) produced a strong argument against this notion. They conjectured that if the division of attention to different body parts was the main cause of the bilateral deficit, then not only the simultaneous use of symmetrical muscles should cause the deficit, but also the simultaneous use of muscles anatomically distant from each other. Therefore, they had their subjects exert maximum isometric strength of the left arm and the right leg simultaneously, and they found no deficit in either the leg or the arm, and concluded that the division of attention was not primarily responsible for the bilateral force deficit.

The contribution of the division of attention to the bilateral deficit in RT has not yet been addressed and can be studied directly by means of an electrophysiological correlate of attention, the contingent negative variation (CNV). The CNV is an event-related potential (ERP) that appears between the occurrence of two successive stimuli, such as in a constant-foreperiod RT experiment in which one stimulus is a preparatory stimulus for the response to the other (Walter et al. 1964). It is usually considered that the CNV consists of an early and a late component; the early CNV reflects the processing of the preparatory stimulus (S1) whilst the late CNV reflects expectancy, attention to the response stimulus (S2), and preparation of the response. With this experimental design it is impossible to distinguish between the attention to the upcoming S2 and the preparation of the required response (for a discussion see Brunia 1993). Division of attention decreases the CNV amplitude (Tecce and Hamilton 1973; Tecce and Scheff 1969). Tecce et al. (1976) found some evidence that CNV magnitude has a positive and monotonic relationship with the level of preparation for response to S2. If the bilateral deficit during a simple RT task is related to division of attention, the magnitude of CNV in conventional, monopolar recordings should decrease for bilateral RT trials compared with unilateral ones. The first purpose of this study was to compare the CNV amplitude during unilateral and bilateral simple RT tasks and to investigate to what extent the division of attention contributes to the bilateral deficit in RT tasks.

As another possible mechanism of bilateral deficit, mutual interhemispheric inhibition, related to the double motor command, has been discussed. Garry and Franks (2000) “proposed that RT increases during some bilateral movements as a result of callosal inhibitory mechanisms” (p 242). Oda and Moritani (1996) showed a reduction of the peak amplitude of the motor potential, significant for the right hemisphere only, for bilateral compared with unilateral exertion in maximal isometric handgrip. However, no electrophysiological evidence that the bilateral deficit in RT is caused by a mutual interhemispheric inhibition has been reported. The second purpose of this study was to assess directly the involvement of both hemispheres in bilateral movement. With this aim we compare the magnitude of response-locked EEG activities in unilateral and bilateral RT tasks. For this purpose we estimated the surface Laplacian of the potential field in order to investigate the contribution of each sensorimotor cortical hand area to the triggering of unimanual and bimanual responses.

The surface Laplacian was estimated by the source derivation method (Hjörth 1975; MacKay 1983). The topographical inferences derived from this computation are relatively free from activities issuing from remote sources (Gevins et al. 1987; Katznelson 1981). Moreover, the Laplacian derivation is particularly suitable for analysing the time course of brain activities, since it provides more reliable measures than conventional monopolar recordings for the latencies of peaks and troughs (Law et al. 1993). Use of the Laplacian operator greatly enhanced the spatial discrimination and revealed the contribution of the sensorimotor cortices during preparation and execution of the response movement (MacKay and Bonnet 1990; Vidal et al. 1995).

Materials and methods

Subjects

Twelve right-handed subjects (six women), aged 22–35 years, were paid for their participation in the experiment. Before the studies, all the subjects gave their informed written consent according to the Declaration of Helsinki. They were informed of the purpose and procedure of the experiment before participating.

Procedure

Subjects were comfortably seated in an electrically shielded and sound-attenuated room, in front of a black panel on which three light-emitting diodes (LEDs) were arranged in a horizontal line. The whole stimulation display subtended a visual angle of about 1.5°. The central LED, used as fixation point, was blue, and the lateral LEDs, used for precue and response signals, could be either red or green. Subjects put their right and left index fingers on the right and left push-buttons, located 25 cm apart on a pull-out table.

Each trial started by illuminating the central fixation LED. One second after, a preparatory signal (S1) was presented for 200 ms. It was composed of both a high-tone auditory signal (1000 Hz), and the onset of the lateral LEDs which gave prior information on the forthcoming response (see prior information section). The response signal (S2) was presented 2.1 s after the S1. A button press turned all the lights off (Fig. 1 *top*). RTs were measured to the nearest millisecond.

The subjects could stop the series whenever they wished by pressing a central push-button positioned in between the two response push-buttons. Therefore, the subjects could blink, swallow, or move between the trials, and if they felt tired, they could have breaks.

Task

In order to keep the stimulation intensity as constant as possible across the various conditions, the two lateral LEDs were always lit, red or green, in all conditions. Half of the subjects (three women and three men) had to respond to the onset of the red colour, in this case the green colour meant “no response”. In the case of responding to red, the subjects had to respond with the right index if the right LED was red, and to respond with the left index finger if the left LED was red. These trials were named “unilateral RTs”. When both LEDs were red, the subjects had to give a synchronous bilateral response with the right and left index fingers. These trials were named “bilateral RTs”. When both right and left LEDs were green, they had to make no response. These trials were named “catch trials” (Fig. 1 *bottom right*).

In simple RT trials, depending on the conditions, the two LEDs were illuminated red and/or green, as S1, thus giving prior information concerning the response to be performed after S2, and indicating which response was to be prepared. Three conditions were defined. Consider the case where the subject had to respond to the onset of the red colour. When the right LED was presented in red and the left LED was presented in green, they indicated unilateral right response, and when the left was red and the right was green, they indicated unilateral left response. When both right and left LEDs were presented in red, they indicated bilateral response. The S2 repeated the information given by S1 in 80% of the trials. The remaining 20% of the trials were NoGo (catch) trials. In these trials the LED which was presented in red as S1, was presented in green as S2. This percentage of NoGo trials was introduced to suppress the anticipation trends, due to the high level of the tem-

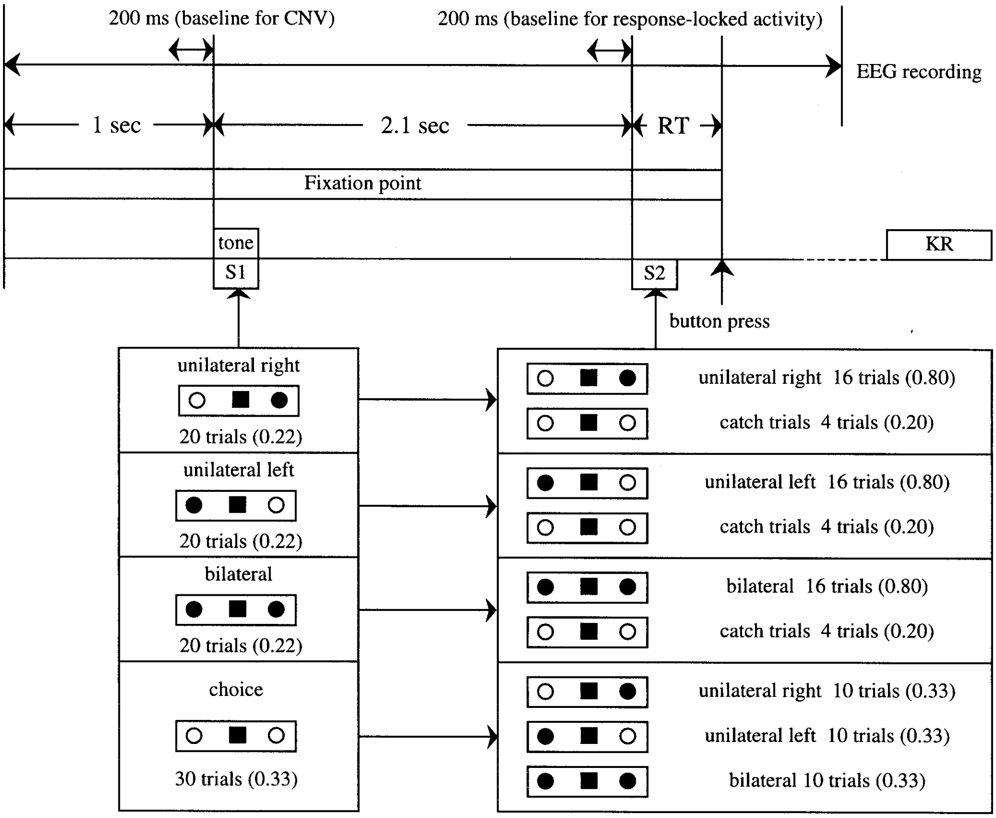


Fig. 1 *Top* Time course of a single trial. *S1* Preparatory signal, *S2* response signal, *RT* reaction time, *KR* knowledge of results. *Bottom left* Condition of information. ■ Light-emitting diode (LED) for fixation point. The two side LEDs were illuminated red (●) and/or green (○), which could tell the subject which response was to be prepared or give no prior information on the response to be performed. *Bottom right* Response signal in unilateral right, unilateral left and bilateral conditions. The S2 did, or did not (catch trial), repeat the information given by the S1. *CNV* Contingent negative variation

poral constraint, in the context of simple RT with a fixed preparatory period duration.

In choice RT trials, in the case where the subject had to respond to the onset of the red colour, both LEDs were presented in green as S1 (Fig. 1 *bottom left*), thus giving no prior information concerning the response to be performed after S2: right, left or bilateral.

For each response condition, right, left or bilateral, there were 16 simple, 4 catch, and 10 choice RT trials. Thus a block consisted of 90 intermixed trials. Although the task was very easy, preliminary learning was organised in order to improve the preparatory set and reduce the RT variance. Reduction of variance made the response-locked ERP processing more powerful. The maximal RT limit was progressively fixed at 400 ms (450 ms for two subjects). To reach this objective, subjects performed three to six training blocks, each on a different day. The experimental session comprised two blocks of trials.

Knowledge of results

Visual feedback was given on a computer screen situated above the LEDs. It was delivered 1 s after the response. If the response was correct and the RT was in the 100–400 ms range, the word “OK” was presented. When the response was wrong, the word “ERREUR” was presented. When the response happened before the S2 or when the RT was shorter than 100 ms the word “ANTICIPATION” was presented. When the RT was longer than 400 ms (450 ms for two subjects), the words “TROP LENT” (“too slow” in French) were presented. When the difference between the RTs of right and left sides was larger than 30 ms in the bilateral RT task, the words “PAS SYNCHRONE” were presented. In the case of “ERREUR”, “ANTICIPATION”, “TROP LENT” and “PAS SYNCHRONE”, the trials were rejected and were repeated randomly during the block. When the response happened in a NoGo trial, the word “PIEGE” (“trap” in French) was presented and the trial was rejected.

Electrophysiological recordings

The EEG activity was recorded at 16 locations by mean of Ag/AgCl electrodes fixed on the scalp. The reference was placed at the right mastoid apophysis and the ground was located on the left mastoid apophysis. The impedances were kept under 5 kΩ (at 30 Hz). The EEG signals were fed into Grass P511 amplifiers and digitalised on-line (bandwidth 0.01–100 Hz, 6 dB/octave, sampling rate 250 Hz). Fifty calibration pulses (50 µV) were injected through the electrodes before and after the experiment. The averaged value served to normalise the data between channels.

The Laplacian was estimated at eight “nodal” electrodes, each placed at the centre of an equilateral triangle formed by three surrounding electrodes, according to MacKay’s (1983) description. Four of them corresponded to the 10–20 system (Jasper 1958): C3, C4, FCz and Fz. Each electrode was separated from its closest neighbour by one-tenth of the mean inion-nasion and tragus-tragus distances, i.e. 3.7 cm on average. Note that such a precise geometrical configuration for each subject is necessary for limiting the spatial noise (Nuñez 1981).

The use of the surface Laplacian reduces blink and eye source contaminations (Law et al. 1993). Otherwise, the Laplacian is very sensitive to the presence of a slow drift affecting one of the monopolar derivations involved in the computation. Considering the characteristic shape of these artefacts, some large eye movements and localised slow drifts were rejected after visual inspection of each trial on monopolar recordings. The percentage of rejected trials on the basis of EEG artefacts was relatively low (16.7%), because after learning subjects became familiarised with the task constraints, and also because the subject could stop the series whenever they wished. The remaining monopolar recordings were averaged and Laplacians were calculated. In order to compare the dynamics of EEG variations across experimental conditions we calculated the slope for the two periods of interest, late CNV and premovement activity. The slope of the Laplacian reflects the speed of activation (or inhibition) for the underlying structure.

During the preparatory period, the brain electrical activity was averaged, time-locked to the preparatory signal, under the four conditions of preparatory information, i.e. unilateral right, unilateral left, bilateral and choice. The base line was the activity during the 200 ms preceding the S1. Response-locked activities were averaged, time-locked to the button presses, for each of the six conditions, i.e. unilateral right, unilateral left and bilateral for simple and choice conditions. The base line was the activity during the 200 ms preceding the S2. In the bilateral conditions, averages were time-locked to each hand, sequentially; to the right-hand responses for comparison with the unilateral right responses and to the left-hand responses for comparison with the unilateral left responses.

Results

Erroneous responses

All conditions included, the rates of anticipations and of too late responses were 0.1% and 2.0%, respectively. The percentage of erroneous responses in catch trials was 15.6% for unilateral left, 16.7% for unilateral right and 14.6% for bilateral. This indicates a high degree of motor preparation. The percentage of incorrect key presses in choice RTs was 2.8%. In bilateral conditions, the rate of non-synchronised responses was 2.5%.

Synchronisation gap

The synchronisation gap was quantified in two ways:

1. We computed the time between right and left key presses. A positive difference means that the right response was given before the left one. This permits us to quantify the mean and the variance of the synchronisation gap.
2. We computed the ratio between the number of trials when the right response occurred first and the number of trials when the left response occurred first.

The synchronisation gap was found to be 6.6 ms (SD 6.3) for the simple condition, and 2.3 ms (SD 8.6) for the choice condition. This difference was statistically reliable [$t(11)=2.64$, $P<0.05$]. Furthermore, the value differed from zero for the simple condition [$t(11)=3.61$, $P<0.01$], whereas for the choice condition the value did not differ from zero [$t(11)=0.93$, not significant (n.s.)]. The analysis of the right-first/left-first ratio showed that the right response was more often given before the left one in simple situations (71/29%; $\chi^2=61.76$, $P<0.01$), whereas both hands responded equiprobably first in the choice condition (55/45%; $\chi^2=2.01$, n.s.).

Reaction time

Reaction times for each hand and each condition are presented in Table 1. A three-factor repeated-measures analysis of variance, with two hands × two response conditions (unilateral vs bilateral) × two conditions of advance information (simple vs choice) was performed, in which the error term was the interaction between the subjects and the factor under analysis. Subjects were faster for simple (257 ms) than for choice RT (321 ms) [$F(1,11)=163.2$, $P<0.001$], which indicates high preparation efficiency. The right-hand RTs (285 ms) were, on average, faster than the left-hand RTs (293 ms) [$F(1,11)=14.32$, $P<0.025$]. As a main effect, the difference between the unilateral (285 ms) and the bilateral (293 ms) response conditions (by chance, identical values to the previous results), did not reach the statistical threshold [$F(1,11)=4.53$, $P<0.10$]. But, the analysis revealed a significant interaction between hand and response conditions [$F(1,11)=9.70$, $P<0.01$]. For the right-hand responses, there was a “bilateral deficit” in RT, i.e. bilateral RTs (291 ms) were significantly longer than unilateral RTs (278 ms) [$F(1,11)=8.95$, $P<0.025$]. For the left-hand response, the small deficit (4 ms) was not significant [$F(1,11)=0.95$, n.s.].

Table 1 Means (*M*) and standard errors of mean (*SEM*) of reaction time (*RT*; ms)

	Simple RT		Choice RT		Mean
	M	SEM	M	SEM	
Right					
Unilateral	247.5	5.2	309.1	6.5	278.3 *
Bilateral	257.3	5.5	324.8	8.1	291.1
Left					
Unilateral	259.3	5.6	323.4	6.7	291.4 (n.s.)
Bilateral	263.7	5.7	327.1	7.2	295.4
Mean	257.0	**	321.1		

*$P<0.05$
**$P<0.01$

Contingent negative variation

In the raw data (monopolar records), due to volume conduction, topographical inferences are not reliable (Katznelson 1981). Law et al. (1993) demonstrate the possibility of improving spatial and temporal resolution in evoked EEG responses using surface Laplacians. To make a thorough comparison of monopolar and Laplacian derivation is not our objective here. In fact we present some monopolar data in order that a comparison be possible with usual data.

Monopolar CNV

Preparatory processes for the four different advance information conditions (simple left, simple right, simple bilateral and choice) were compared. Amplitude variations according to experimental factors were relatively similar for each location because of volume conduction (Fig. 2).

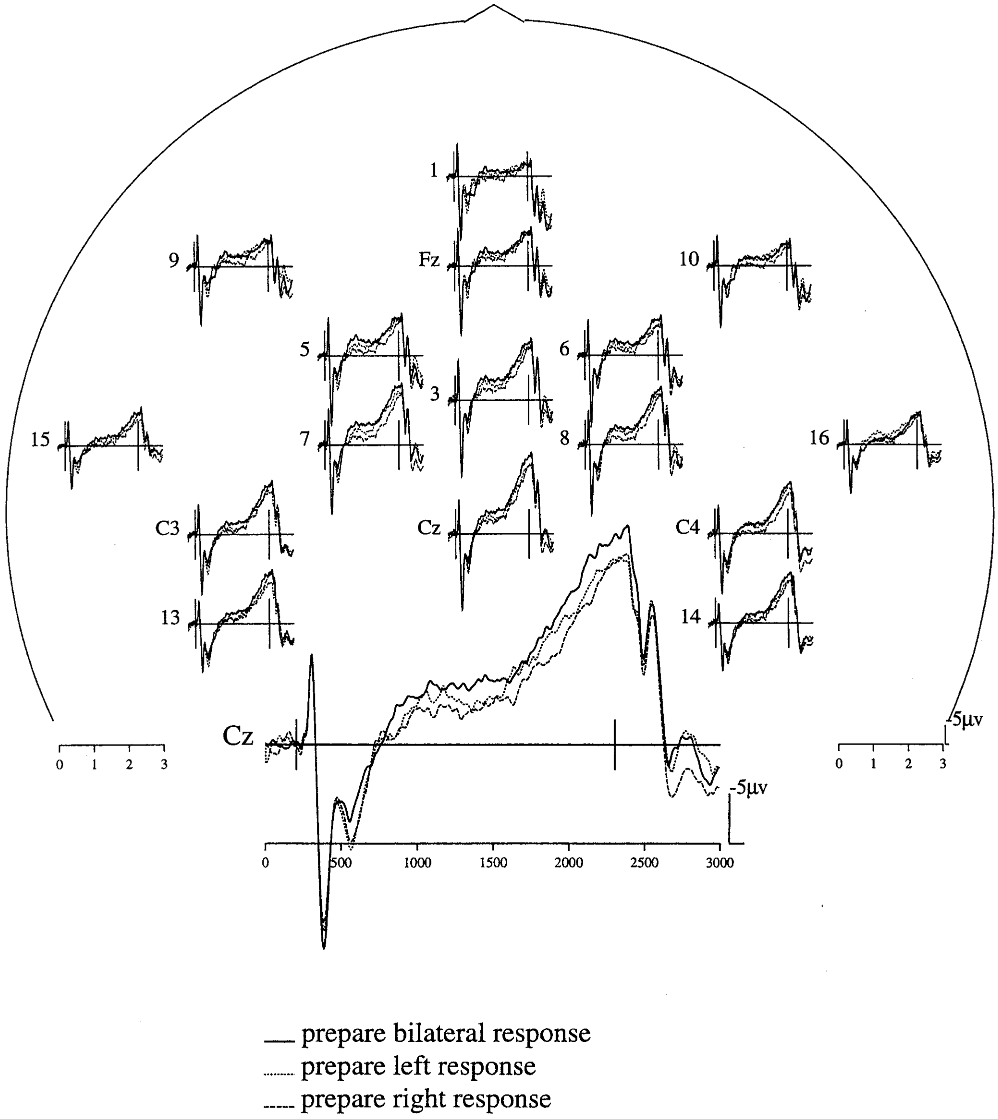


Fig. 2 Conventional monopolar recordings. Grand average of the CNV during the preparatory period, in the simple RT task, for the bilateral, the unilateral left and the unilateral right conditions. On the *abscissa*, the *first vertical bar* indicates the preparatory signal and the *second vertical bar* indicates the response signal (2100 ms preparatory period). *Inset* Enlargement for the Cz location

The maximal CNV amplitude was in the central region which reproduces typical data. A statistical comparison between conditions was done for the Cz location (Fig. 2 *inset*), where amplitude variations were the highest. There were significant differences between the four conditions [$F(3,33)=3.81$, $P<0.05$]. For the simple RT condition, the difference observed during the preparation for the bilateral vs unilateral response, although not significant [$F(1,11)=4.28$, $P<0.10$], was in the opposite direction than predicted by the division of attention hypothesis. The late component of the monopolar CNV tended to become larger in the bilateral trials. So, in monopolar recordings we did not observe, on the late CNV amplitude, any correlate of the behavioural bilate-ral deficit.

Laplacian CNV

On Fig. 3 are shown the late CNV over the hand sensorimotor areas according to the four preparation conditions. To analyse the dynamics of the preparatory motor activation during the preparation conditions, the slope (expressed in μV cm^{-2} s^{-1}) of the Laplacian late CNVs was calculated over the motor cortices during the 500 ms before the response signal (see Fig. 3). The ANOVA indicated that there was neither significant main effect nor interaction of response conditions and electrode positions (C3/C4).

Motor potentials

To focus on the main point, we limited the topographical analysis to C3 and C4, over the hand areas of the sensorimotor cortices (Homan et al. 1987), to assess a possible bilateral deficit. In Fig. 4, the grand average of Laplacian response-locked activities over C3 and C4 are presented in simple and choice RT conditions. First, in unilateral responses, we compared contralateral and ipsilateral motor cortices (Fig. 4a). Second, over the contralateral mo-

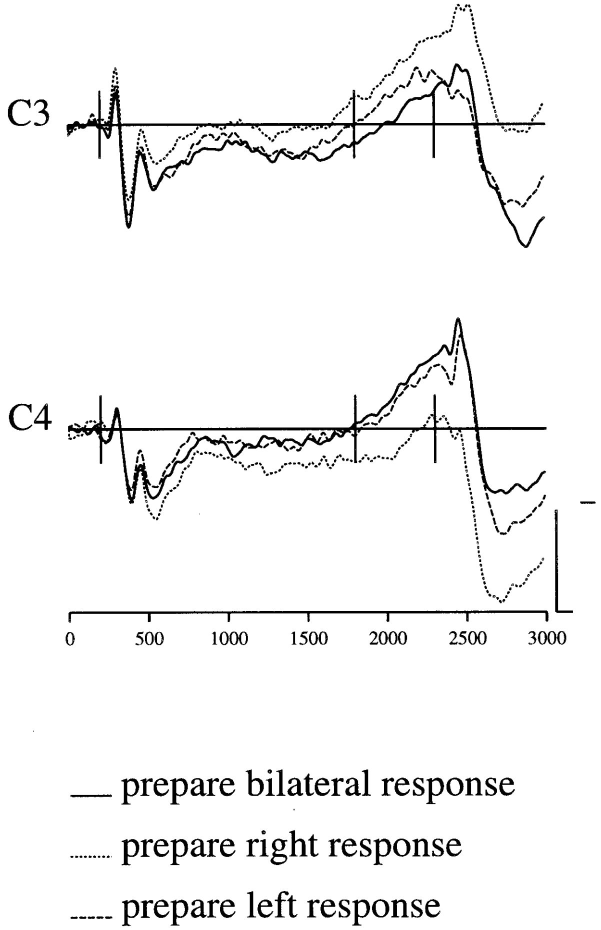


Fig. 3 Laplacian over C3 and C4 during the preparatory period for unilateral left, unilateral right and bilateral responses in the simple RT condition. On the *abscissa*, the *first vertical bar* indicates the preparatory signal, the *third vertical bar* indicates the response signal. The slope of the CNV-like was calculated between the *second* and the *third vertical bars* (from –500 to 0 ms before the response signal). On the *ordinate*, the amplitude of the Laplacian (*vertical bar*=–0.5 μV cm^{-2})

tor cortex, we compared unilateral and bilateral commands (Fig. 4b).

In unilateral responses, at the time of the motor command, i.e. from –100 to –50 ms preceding the press on the push-button, which is about the moment of the electrical muscular activity onset, the Laplacian derivations allowed a dissociation: (1) a negative wave developed over the contralateral motor cortex (maybe equivalent to the premovement negativity or motor potential commonly observed with the standard method) and (2) a positive shift developed over the ipsilateral motor cortex. The clearest divergence appeared in choice RT condition for the right response (Fig. 4a).

To evaluate the dynamics of the motor cortex activity on the response-locked EEG, we calculated the slopes of the Laplacian, expressed in μV cm^{-2} s^{-1}, during the phasic changes visible at the time of the voluntary control, i.e. between –100 to –50 ms before the press on the push-button (Fig. 4a).

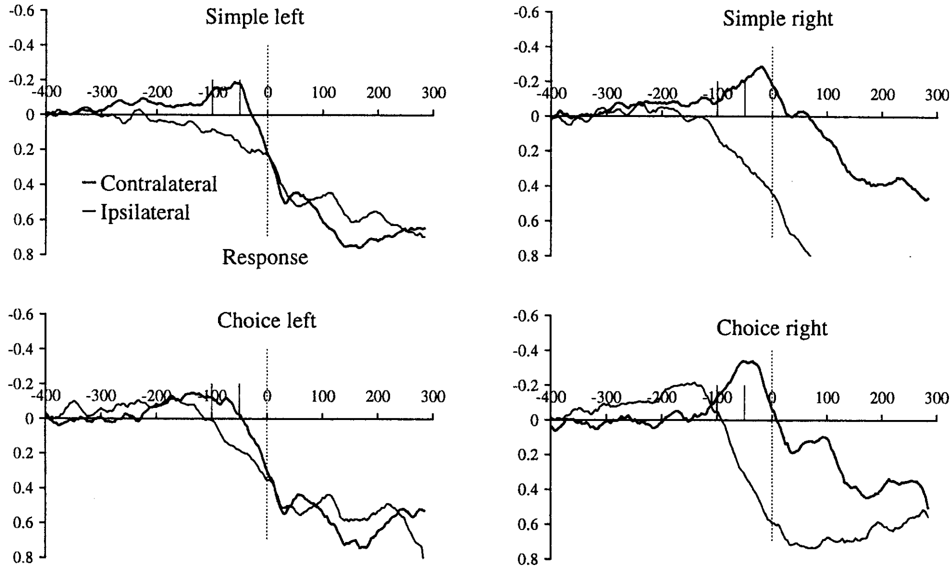
The first statistical analysis concerns the ipsilateral vs contralateral slope divergence for unilateral responses. The three-factors ANOVA includes two hemispheres (contralateral vs ipsilateral) × two task conditions (simple vs choice) × two hands (right vs left). The slope was strongly dependent on its position, contralateral vs ipsilateral, relative to the response index finger side [*F*(1,11)=25.18, *P*<0.001]; neither the task condition, simple vs choice [*F*(1,11)=3.21, n.s.], nor the hand factor [*F*(1,11)=0.27, n.s.] were significant. The analysis revealed a first-order interaction between hemisphere involvement and hand [*F*(1,11)=7.45, *P*<0.025]. That is, the slopes of the contralateral vs ipsilateral Laplacian time courses were strongly divergent for the right index response [*F*(1,11)=19.92, *P*<0.001], but not for the left one [*F*(1,11)=1.60, n.s.]. Seeing that the second-order interaction was also significant [*F*(1,11)=4.88, *P*<0.05], we looked at the "hemisphere × hand" interaction for the choice and simple task conditions separately. The interaction was significant in the choice RT condition [*F*(1,11)=9.20, *P*<0.025], but not in the simple one [*F*(1,11)=1.91, n.s.]. This means that the divergence contralateral vs ipsilateral was actually stronger for the skilful right hand in the choice RT condition only, i.e. when the subjects could not prepare the response.

In the second analysis we compared the slope of the negative wave over the contralateral sensorimotor cortex for unilateral and bilateral responses (Fig. 4b). The three-factors ANOVA included two response conditions (unilateral vs bilateral) × two task conditions (simple vs choice) × two hands (right vs left). On average, a bilateral deficit appeared. The slopes were stronger for unilateral than bilateral responses [*F*(1,11)=8.85, *P*<0.025; Fig. 4b]. There was no significant main effect either according to the task condition [*F*(1,11)=1.24, n.s.] or to the hand [*F*(1,11)=3.89, n.s.], and no significant interaction. However, as the bilateral deficit in RT was significant for the right hand only, we tested each hand separately. For the right-hand response (Fig. 4b *right column, C3*), the slope was actually stronger for unilateral than bilateral response [*F*(1,11)=14.37, *P*<0.01]. For the left-hand response (Fig. 4b *left column, C4*), the difference was not significant [*F*(1,11)=2.61, n.s.]. Therefore, for the right index finger response, we observed simultaneously a behavioural deficit in RT and a reduction of the dynamics of the response-locked Laplacian over the contralateral (involved) motor cortex.

Discussion

To better understand the relative deficit observed in bilateral RT, we investigated the dynamics of the motor cortex EEG activities, over C3 and C4, during the preparatory and execution periods of unimanual and bimanual responses in simple and choice RT tasks. The source derivation method was used to calculate an approximation to the surface Laplacian, in order to reduce remote electrical source influences and to increase the temporal resolution of the EEG (Law

a) unilateral response-locked activity



b) contralateral response-locked activity

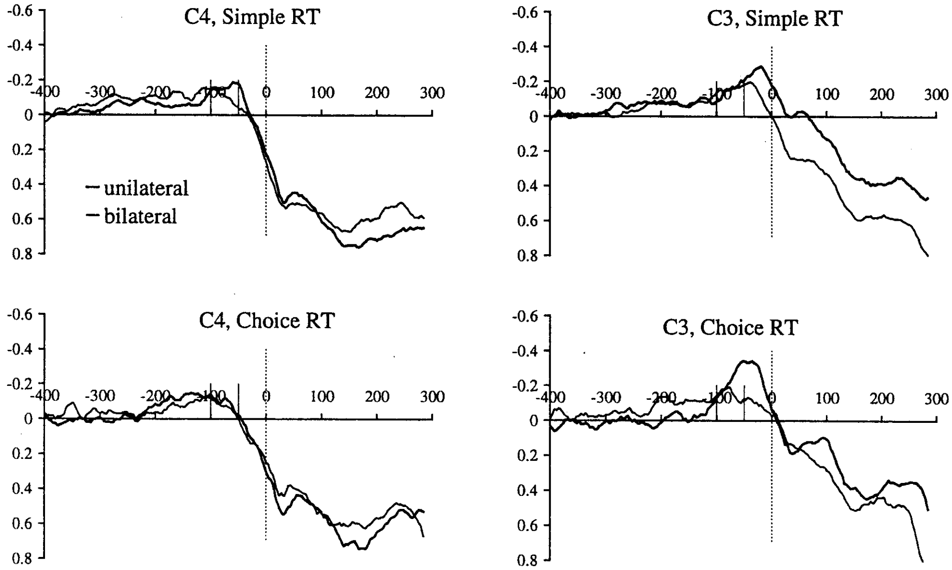


Fig. 4a, b Laplacian for the response-locked activity. On the *abscissa*, the *vertical dotted line* indicates the response execution. The slope of the response-locked activity was calculated from –100 to –50 ms before the key-press (between the *two vertical bars*). On the *ordinate*, the amplitude of the Laplacian in µV cm^{-2}. **a** Activity over contralateral and ipsilateral sensorimotor cortices. On the *left* for unilateral left responses, on the *right* for unilateral right responses. In the *upper row* for the simple RT condition, in the *lower row* for the choice RT conditions. **b** Contralateral activity for unilateral and bilateral responses. On the *left* for the sensorimotor cortex contralateral to the left response (C4), both averages were time-locked to the left key-press. On the *right* for the sensorimotor cortex contralateral to the right response (C3), both averages were time-locked to the right key-press

et al. 1993). This method allowed the contralateral and ipsilateral activities to be well separated. The main results of this experiment may be summarised as follows:

1. At the behavioural level, a deficit in RT was observed for the right hand in the bilateral condition. The right index finger RTs were significantly longer in the bilateral condition than in the unilateral one. The difference was not significant for the left hand. This result confirmed that of Taniguchi (1999) and agreed with previous ones where the bilateral deficit was present for the two hands (Di Stefano et al. 1980; Kerr et al. 1963; Ohtsuki 1981a; Steenbergen et al. 1996).
2. There was no electrophysiological evidence for a preparatory origin of such a bilateral deficit. The slopes of the late Laplacian CNVs, as an index of the motor preparation, appeared no different for bilateral and unilateral conditions.

3. For unilateral movements, at the time of the motor command, the sensorimotor cortices showed an opposite electrical activity. A phasic negativity increased over the contralateral cortex and simultaneously a phasic positivity increased over the ipsilateral cortex.
4. During the period of execution, a relative diminution of the negative wave, now over both hemispheres, was observed, contemporaneous with the bimanual motor command. This decrease, probably due to the effect of an interhemispheric inhibition, might be a determining factor of the deficit in the bilateral RT condition.

Absence of deficit in late CNV

Since a specific motor preparation was impossible during our choice RT condition, we have considered the relationship between RT and the preceding late CNV in the simple RT condition only. According to Tecce et al. (1976), the size of the late CNV potential has a positive and monotonic relation to attention involved in the task. Thus if the bilateral deficit is caused by a division of attention, the magnitude of monopolar CNV should decrease during the preparatory period for bilateral compared to unilateral RT trials. However, in our conventional monopolar recordings, there was no difference between the amplitude of the late CNV in the bilateral condition and in the unilateral condition. Thus, if we accept Tecce's proposal, the bilateral deficit is unlikely to be due to a division of attention during motor preparation.

The Laplacian computation allows to analyse EEG activity of limited brain regions (Katznelson 1981). Over the hand areas of the sensorimotor cortices, the late Laplacian CNV showed a negative shift that started about 500 ms before the response signal (Fig. 3). The slope of the late Laplacian CNV, used as an index of the specific motor preparation, was no different in bilateral and unilateral conditions. In conclusion, there was no argument in the data for a preparatory origin of the bilateral deficit, in the simple RT task.

Bilateral deficit in the response-locked activity

A bilateral deficit was found to exist in the electrical activity related to the motor command. Considering the hemisphere contralateral to the index finger response, the response-locked Laplacian activity revealed that the motor potentials were smaller for the bilateral than for the unilateral responses. This was significant for the right-hand response only, as for the RT data. These results confirm, in an RT task, those obtained by Oda and Moritani (1995) who analysed movement-related cortical potentials over the motor cortex areas. They reported that a bilateral deficit in isometric force and EMG activity was associated with a reduced peak amplitude of the motor potential. Such a reduction is likely to be the cause of the bilateral deficit in the RT task. A reduced motor potential amplitude suggests a reduced intensity of the corticospinal command, leading to a reduced corresponding EMG activity. It is known that in RT tasks, a decrease in the rising time of the EMG leads to an increase of the motor time, i.e. the time between EMG onset and mechanical onset (Hasbroucq et al. 1995).

In brief, the bilateral deficit, both in RT and force, seems to be due to a reduction of the motor command. Thus, the bilateral deficit is motor in nature. The origin of such a deficit in the bilateral motor command can perhaps be found in the persistence of a transcallosal inhibitory activity. Such an inhibition affects the motor cortex of the alternative response in the unimanual RT condition. At the time of the double motor command, in the bilateral RT condition, a double, mutual inhibition could be produced. In the following paragraph are detailed the simultaneous occurrences of a contralateral activatory activity and of an ipsilateral inhibitory activity, over the sensorimotor cortices.

Asymmetry of sensorimotor cortex activity in right-handed subjects

At response time, over the sensorimotor cortex, the slope of the response-locked activity was negative, or relatively more negative, for the involved contralateral motor cortex. This negativity probably reflects an increasing activation of the underlying structures in charge of the correct response. It corresponds to the premovement negativity or motor potential commonly observed with the standard EEG method. On the contrary, the corresponding slope was positive for the ipsilateral motor cortex. Assessed by the source derivation method, this reverse evolution has already been observed (Bonnet et al. 2000). The positivity of the slope reflects an increasing inhibition of the alternative incorrect response. Such inhibitory activity may be the result of an interhemispheric transcallosal inhibition which was demonstrated in animal experiments (Asanuma and Okuda 1962) and in humans by using transcranial magnetic stimulation (TMS; Ferbert et al. 1992). With double TMS, Di Lazzaro et al. (1999) observed the suppression, by the conditioning stimulation of (for instance) the left hemisphere, of both the descending spinal cord volley and the EMG responses evoked by the test stimulation of the right hemisphere. They concluded that TMS of the motor cortex on one side in man can evoke activity in the transcallosal pathway producing an inhibition of the contralateral motor cortex.

The fact that the hemispheric asymmetry was most prominent for the right-hand responses was attributed to the motor lateralisation of our right-handed subjects. Many results in the motor control literature support the notion of differences in the hemispheric control of right- and left-hand movements, in right-handers, in favour of the left hemisphere, i.e. in favour of the right hand. Netz et al. (1995) using TMS conditioning stimulus to one hemisphere about 10 ms prior to the test stimulus to the opposite hemisphere demonstrated that ‘in right-handers, the inhibition after stimulation of the “dominant” left-hemisphere was more marked than after stimulation of the “non-dominant” right hemisphere’ (Netz et al. 1995, p 527). Our EEG data confirm this asymmetry which expresses itself also for the inhibition of the sensorimotor cortex ipsilateral to the response hand. The ipsilateral premovement positivity was stronger over the right hemisphere for the right index response than over the left hemisphere for the left index response. In that case the left hemisphere would also be dominant in producing the contralateral inhibition. Such an EEG asymmetry fits the contralateral transcallosal origin of the ipsilateral premovement inhibition.

For a two-hand choice RT condition, the appearance of opposite motor cortical activations is functionally adapted. Indeed, in choice condition, during the preparatory period, the two possible responses are prepared. The production of a unilateral response therefore necessitates: (1) activating the required response and (2) inhibiting simultaneously the alternative one. Such an active inhibition of a symmetrical response seems *a priori* not necessary in the simple RT condition. Nevertheless, although it was weaker in the simple than in the choice condition, such an inhibition was still present when the subjects knew in advance the responding hand. This persistence was perhaps due to the motor context of the task. Indeed, the trial types, simple vs choice and unilateral vs bilateral responses, were mixed during a block of trials. Thus, at the start of the trial, the subjects must switch from one task to the other. In this situation, task set inertia is known to appear (Allport et al. 1994). That is, the task in the previous trial still influences the performance on the current trial. Because of this task set inertia, subjects could not refrain from inhibiting the alternative response, even in the simple RT situation. For the same reason, such an inhibition should also be present in the bilateral task. The bilateral deficit in the command may be the result of the crossing effect of mutual interhemispheric inhibition.

Synchronisation constraint

An alternative interpretation rests on the synchronisation constraint. Indeed, the bilateral deficit might also be due to the supplementary constraint of synchronisation for the bilateral response. As it is assumed generally that actions are controlled by their anticipated effects, the timing of the motor commands became an important factor for synchronised bilateral movements. The performance regarding the synchronisation was not automatically perfect. We noticed 2.5% of erroneous asynchronous responses (i.e. interval >30 ms). In this experiment, the right index finger RTs were on average 9 ms faster than the left index finger RTs. This right–left difference changed according to the task conditions. For unilateral responses, the right–left difference was 12 ms in simple and 14 ms in choice RT, but, for bilateral responses, was 6 ms in simple and 2 ms in choice RT. Then, due to the synchronisation constraint that we introduced and checked, the synchronised bilateral reaction resulted in a slowing down of the right index finger response. Indeed, the bilateral deficit was significant for the right response only. At the level of the involved motor cortex (C3), the expression of such a slowing down could be a reduction of the amplitude of the premovement negative wave. In agreement with this proposal, we observed that the contralateral activation was actually stronger for unilateral than bilateral responses for the right-hand responses only. In any case, the control of the synchronisation, which allows the double motor command, requires supplementary processing. The temporal regulation of the simultaneous activities of the two hemispheres should require a slowing down for the left motor cortex activity, and then a decrease in the dynamics of the negativity over the cortex for bilateral responses.

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