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RESEARCH ARTICLE

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Programming the duration of a motor sequence: role of the primary and supplementary motor areas in man

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Abstract Event-related potentials were recorded in a reaction time (RT) paradigm, where the duration of a learned interval (either 0.7 s or 2.5 s) delimited by two brief button-presses was to be accurately controlled. A preparatory signal (PS) either did not give or gave prior information concerning the duration of the following response (neutral condition or primed conditions, respectively). In the latter case, the information was either validated (valid condition) or invalidated (invalid condition) by the response signal (RS). When duration was not known in advance (invalid and neutral conditions), RTs were longer before a response of short than long duration. This difference was not found under the valid condition. During the preparatory period (PP), the amplitude of the contingent negative variation (CNV) was larger when the duration was primed than when it was not. A larger CNV appeared when the PS primed a short rather than a long duration. This effect occurred in the early part of the PP over the supplementary motor area (SMA) and in its latest part over the primary motor area (MI). The RT and the electrophysiological pattern were interpreted as revealing the occurrence of programming operations regarding the temporal dimension of the response. The time course of the CNV over the SMA and MI suggested that these two areas were hierarchically organized. Between the RS and the onset of the response, differences probably related to programming effects were still found over MI: the activities were larger under the valid than under the neutral condition. However, no sign of deprogramming (expected in the invalid condition) was observed: similar amplitudes were found under the neutral and invalid conditions. Deprogramming operations seemed to be postponed during response execution where the invalid condition evoked larger activities than the two other conditions over the SMA. Finally, MI but not the SMA yielded a Bereitschaftpotential before the second press ending the response (i.e., during response execution). These results suggest that the duration of a motor response can be a part of the motor program and that the SMA plays a major role in programming processes but not in response execution, contrary to MI.

Key words Timing task · Motor program · Brain potentials · Supplementary motor area · Primary motor area · Source derivation · Human

Introduction

Any action takes time. However, only when the duration of an action must be accurately timed does it seem to require specific control. Time production tasks are appropriate in the study of how this control takes place. A major avenue by which to establish that the duration of a response is liable to be centrally controlled is to show that this duration is part of the motor program, in other words that it can be programmed before response execution.

Centralist conceptions of motor control imply that a plan of intended actions must be elaborated before movement onset (Paillard 1960). This planning results in a set of abstract instructions, called a motor program, thought to pre-specify explicitly certain characteristics of the response to be produced (Keele 1968; Schmidt 1975; Requin 1980). The parametric model of motor programming, in its most restrictive version (Rosenbaum 1983, for a review), postulates that motor program instructions specify separately the physical descriptors of the response such as direction, effector, amplitude and speed (but see Rosenbaum 1980; Bonnet et al. 1982; Spijkers 1987; Lépine et al. 1989; Bonneviale and Thon 1990), although the evidence has been a matter of debate (Goodman and Kelso 1980; Dornier and Reeve 1990).

Few studies have delt with the possible specification of duration as a relevant parameter. Klapp et al. (1974), with durations of 150 to 600 ms, showed that reaction time (RT) was shorter before a key press of short rather than long duration when the duration to be produced was

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not stipulated before the response signal (RS). When a preparatory signal (PS) indicated in advance (i.e., precued) which duration was to be executed after the RS, no RT difference was found between the two conditions. The authors suggested that the differences in RT revealed differences in the times needed to program a short and a long response. The absence of such an effect in the duration-precued condition indicated that the programming operations had taken place in the preparatory period (PP), between the PS and the RS, and, consequently, did not influence RT.

Klapp and Erwin (1976) replicated these effects but failed to find them for durations longer than 600 ms. The authors suggested that only very brief durations could be programmed before response execution. According to Klapp (1977), this is due to the fact that, when a response is very short, its cessation must be prepared before movement initiation. If this interpretation is valid, the observed programming effects should result from the programming of some mechanical/dynamical characteristics of the response closure rather than from the programming of the response duration itself. However, Vidal et al. (1991) found programming effects for short (0.2 s and 0.7 s) as well as longer (0.7 s and 2.5 s) durations. Thus, even those durations which appear to be long enough to enable response closure processes to take place during execution are liable to be programmed. This assumption has also been sustained by neurophysiological data: Macar et al. (1990) found that the level of electrical brain activity over the supplementary motor area (SMA) was higher during the PP when duration was precued than when it was not.

These results raise several questions. First, one could argue that the duration of the response can be controlled indirectly through its dynamical parameters, for instance the level of the applied force. To preclude this possibility in the following experiment, subjects had to produce short or long intervals delimited by two brief button-presses. Second, a priming paradigm was used to study programming operations further and check whether changes in programming would affect the RT. In a priming paradigm (Rosenbaum and Kornblum 1982), the RS will not only provide a "go" signal but will also indicate that the prepared response must be altered on invalid trials. Hence, in those trials, the motor program must be updated after the RS, and RT may be expected to reflect the cost of deprogramming and reprogramming operations.

In addition to RTs, the brain potential changes occurring before and after the RS were analyzed in relation to the particular programming operations induced by the various categories of trials, which could provide either valid, invalid or no information concerning response duration. During the PP of a priming paradigm, the main sustained electrical change that can be observed in brain activity is the contingent negative variation (CNV; for review see Birbaumer et al. 1990). Here, CNV amplitude was taken as an indice of activation of the recorded cortical areas and the level of activation was evaluated as a function of programming operations. The potentials evoked by the signals (PS and RS) and the response-dependent activities were analyzed.

Materials and methods

Subjects

Twenty-four right-handed subjets were paid for their participation in the experiments (11 women and 13 men). All subjects yielded behavioral data, but only 15 of them underwent electrophysiological recordings. In 3 subjects, the recordings were excluded from the analysis because of various artifacts. In sum, the behavioral data were obtained from 24 subjects and the electrophysiological data from 12 of them.

Subjects held a push-button in their left hand. They were comfortably seated in an electrically shielded and sound-attenuated room, in front of a white panel on which were secured four green light-emitting diodes (LEDs) arranged in a square. Ten electrodes (Ag/AgCl; Comepa) were glued onto the subject's scalp with a conductive paste.

Training

First, the subjects were trained to produce accurate durations. The training session began with the presentation of five successive pairs of tones. Each pair was separated by the "target" duration, which provided the model for response production. After the fifth presentation of the model, the subjects tried to reproduce the proper duration and checked their performance on the basis of visual feedback, until eight correct responses were emitted in the ten last responses. Then, training for the second duration was provided. The order of presentation of the durations was counterbalanced between subjects. Two subjects were eliminated at this early experimental stage because they were unable to fulfill the requirements after 45 min of training.

Knowledge of results

Visual feedback was given on a computer screen situated above the LEDs. It was delivered 1 s after the end of the response. If the interval was correct (less than 7.5% longer or shorter than the target), the word "bien" ("right" in French) was presented. When the duration produced was too long or too short (7.5–22.5% longer or shorter than the target) the words "trop long" or "trop court" ("too long" or "too short") were presented, respectively. When the duration produced was excessively short or long (more than 22.5% shorter or longer than the target) "trop long" or "trop court" were flashed repeatedly and the trial was rejected. Knowledge of results was given after each trial.

Task

(Fig. 1): As soon as possible after the RS, the subjects had to initiate an interval delimited by two short (<300 ms) button-presses produced with their left thumb. The RS was preceded, 2 s earlier, by a PS of 1 s duration. Two different intervals could be required: short (0.7 s) or long one (2.5 s).

The target interval was signaled by the four green LEDs located at the corners of a virtual square (visual eccentricity <1.5°). In half the subject group, the upper LEDs represented a 0.7-s duration, and the lower ones represented a 2.5-s one, and vice versa in the other half of the group. During a trial, the subjects were instructed to gaze at a fixation point located in the center of the LED square. They were requested to avoid swallowing, moving their head or eyes, and blinking. The subjects initiated a trial by briefly pressing the push-button.

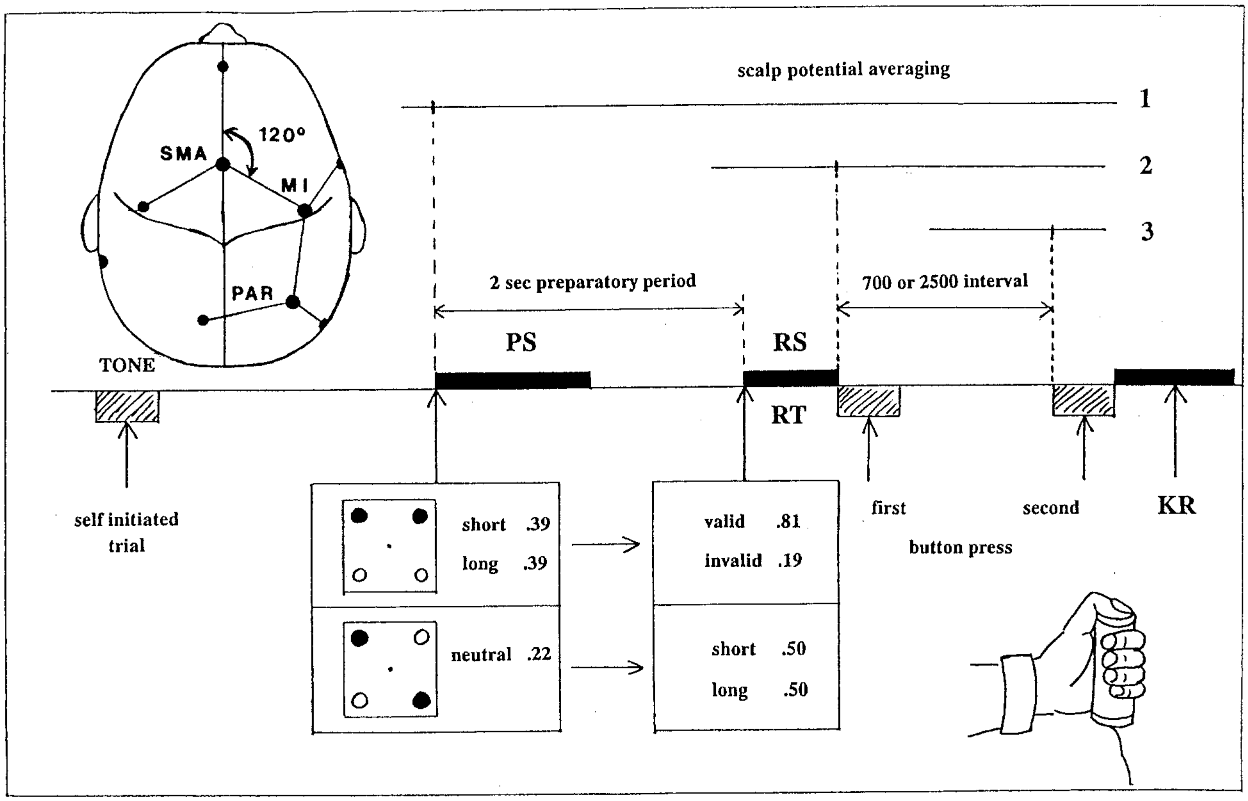


Fig. 1 *Top left* Electrode placement: supplementary motor area (*SMA*), primary motor area (*MI*), and parietal area (*PAR*) indicate the three positions where the surface Laplacian could be estimated; the distance between adjacent electrodes was one-fifth of the inion-nasion distance. *Top right* Time course of a single trial: The *black bars* represent the lighting periods of the signals. (*PS* preparatory signal, *RS* response signal, *RT* reaction time, *KR* knowledge of results). *Bottom* LED configurations used to deliver the instructions (with probability of occurrence); examples of LED lighting (with lit LEDs marked by *black dots*) are given in a primed condition (*top*) and in condition Neutral (*bottom*)

Conditions of information

Depending on the trials the PS could:

1. Tell the subject which duration was to be prepared. The two upper or the two lower LEDs were illuminated. According to the duration cued by the PS, two conditions (condition Short and condition Long) were defined during the PP.
2. Give no prior information on the duration to be produced (condition Neutral). In half the trials, the right superior and left inferior LEDs were lit and vice versa in the other half.

In conditions Short and Long, the RS confirmed the information given by the PS in 81% of the trials (condition Valid) or invalidated it in 19% (condition Invalid): for each duration, there were 85 Valid, 30 Neutral, and 20 Invalid trials, for a total of 270 trials. The different conditions were intermingled. After the training on durations, 50 practice trials that included all of the conditions were provided before the experimental trials. The subjects were free to perform the task at their own pace: the subject himself made each trial start. Therefore, the subjects could blink, swallow, or move between the trials and, if they felt tired or bored, they could have breaks.

Behavioral measures

RT and response duration were measured with a 1-ms precision. Trials were rejected when RT were less than 100 ms or greater than 800 ms. Trials were also rejected when the produced duration was more than 22.5% shorter or longer than the target duration.

Electrophysiological recordings

The surface Laplacian of the electrical activities was computed by the source derivation method (Hjorth 1975). The topographical inferences derived from this computation are known to be relatively free from artifacts (Katznelson 1981; Srebro 1985; Gevins et al. 1987; Perrin et al. 1987; Vidal et al. 1992). Moreover, the surface Laplacian is particularly suitable for analyzing the temporal course of brain activities, since it provides more reliable measures than conventional monopolar recordings for the latencies of peaks and troughs (Law et al. 1993b). The Laplacian computation required the electrodes to be focused on a limited brain region: they were placed over the right hemisphere, given that the subjects responded with the left hand. The motor activity recorded on the right hemisphere was assumed to be free from contamination by the mental verbalizations possibly induced during the PP by the different conditions of information.

The brain structures underlying the electrodes were identified on the basis of the information provided by Homan et al. (1987) and Steinmetz et al. (1989). The Laplacian was estimated at three "nodal" electrodes. Each nodal electrode was surrounded by three electrodes, according to MacKay's (1983) description. Because of the triangular organization needed for electrode placement (Fig. 1), several electrode positions did not correspond exactly to the 10–20 system (Jasper 1958). Each electrode was separated from its closest neighbor by one-fifth of inion-nasion distance. Each nodal electrode was placed at the center of a virtual equilateral triangle, formed by three surrounding electrodes. The first nodal electrode was placed at FCz, situated over the SMA. Among the electrodes surrounding it, the one situated on its right and very close to C4 (slighthly anterior and superior to C4) constituted a second nodal electrode: it was located over the primary motor area of the superior limb (MI). One of the electrodes surrounding MI constituted the third nodal electrode situated over the superior parietal area (PAR).

The activity recorded by the eight electrodes was fed into Grass P511 amplifiers and digitalized (bandwidth 0.01–100 Hz, 6 dB/octave, sampling rate 250 Hz). Fifty 50-µV calibration pulses were injected through the electrodes before and after the experiment. The averaged value served to normalize the data between channels. The reference was placed at the right mastoid apophyse and the ground was located on the neck.

Rejection of artifacts

The use of surface Laplacian removes eye source contamination (Law et al. 1993a). Nevertheless, eye movements and EMG bursts were first rejected by visual inspection of each trial on monopolar recordings, considering the characteristic shape of these artifacts and the gradients of activity obtained on the different locations. The remaining monopolar recordings were averaged and Laplacians were calculated on the basis of these monopolar means.

Recording periods and baseline

Brain activity was recorded from 100 ms before the presentation of the PS to the end of the response. CNV recordings during the PP were averaged separately under conditions Short, Long, and Neutral and were time-locked to the PS. The baseline was the activity of the 100 ms preceding the presentation of the PS. After the RS, the trials were averaged separately for each duration and each condition, and referred to a baseline corresponding to the last 100 ms of the PP.

Response-related activities were averaged backward, time-locked to the motor responses: (1) during the 600 ms preceding the first button press, those activities were averaged separately for each duration under each condition, and the baseline was the mean level of activity in the preceding 1700 ms. (2) When the interval to be produced was short, response-related activities were analyzed during the 500 ms preceding the second button-press. Trials were averaged separately for each condition and the baseline was the mean level of activity in the preceding 1000 ms. (3) When the interval to be produced was long, the same procedure was applied to the 1500 ms preceding the second button-press. Long baselines were measured in the response-related analyses so as to get rid of the phasic activity differences that possibly occurred before the period of analysis, depending on priming conditions. The analysis of variance applied to the data included two crossed factors: Duration (Short and Long) and Condition (Valid, Invalid, and Neutral).

Results

Reaction time

Figure 2 shows the RTs for each duration under each condition. RTs decreased with the probability of the RS (effect of condition: $F_{2,46}=44.50$, $P<0.001$. Neutral vs Valid: $F_{1,23}=72.15$, $P<0.001$; Invalid vs Neutral $F_{1,23}=4.82$, $P<0.05$) and were shorter before the response of short than of long duration ($F_{1,23}=22.66$, $P<0.001$), especially under conditions Neutral and Invalid. Although the Condition×Duration interaction was not significant ($F_{2,46}=0.70$), the short-long difference was tested under each condition, because previous studies consistently reported that this difference appears when duration is uncued and disappears when duration is precued. Indeed, the short-long difference was significant for the Invalid condition $F_{1,23}=4.72$, $P<0.05$) and the Neutral condition ($F_{1,23}=8.28$, $P<0.01$), but not for the Valid condition ($F_{1,23}=3.93$).

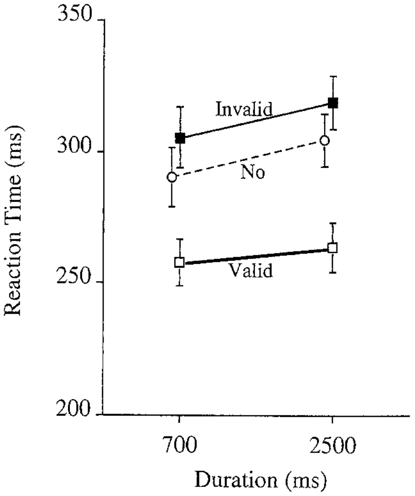


Fig. 2 Reaction time (*ordinate*) of 24 subjects as a function of response duration (*abscissa*) in each priming condition. *Vertical bars* indicate, for each RT value, the standard error of the mean

Accuracy

The accuracy of the interval productions was evaluated by measuring the mean absolute value of the differences between productions and targets, expressed as a percentage of the target duration. There was no significant effect of durations ($F_{1,23}=0.93$) and of priming conditions ($F_{2,46}=0.61$) and no interaction between those factors ($F_{2,52}=1.46$). No short-long difference in accuracy either appeared when the conditions were examined separately as was done with RTs (Valid $F_{1,23}=0.02$; Neutral $F_{1,23}=2.34$; Invalid $F_{1,23}=0.23$).

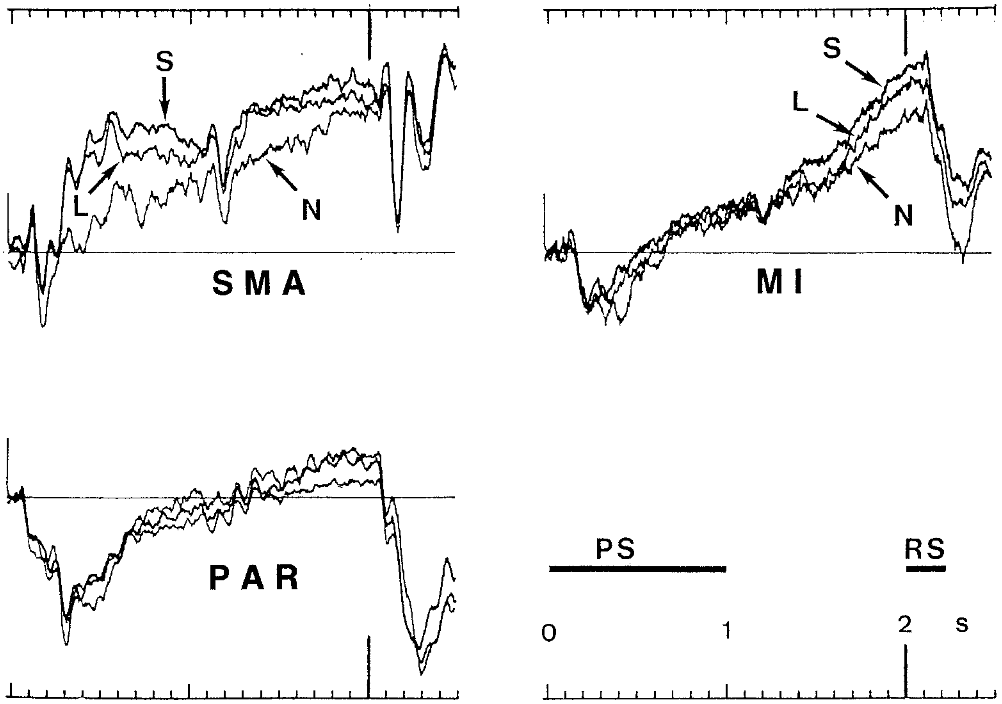
CNV during the PP

CNV amplitudes were estimated by measuring the surface between the level of cortical activity between such experimental condition and the level of the corresponding baseline. In the periods where visual inspection suggested an effect of conditions, those measures were submitted to an analysis of variance. Figure 3 represents the CNVs obtained over the three areas where the Laplacian could be evaluated (SMA, MI, and PAR) under conditions Short, Long, and Neutral.

Over the parietal cortex, no significant difference between conditions was found at any moment of the PP ($F_{2,22}<4.38$ for all the tested periods: last 500 ms, last 300 ms, and last 100 ms of the PP).

Over the SMA, the effect of conditions on CNV amplitude was more prominent in the early part of the CNV. Three periods were considered in detail: (1) In the 300–500 ms following the PS, the effect of conditions was significant ($F_{2,22}=39.87$, $P<0.001$) and was due to the difference between condition Neutral and each of the other conditions (Neutral vs Short, $F_{1,11}=64.94$, $P<0.001$; Neutral vs Long, $F_{1,11}=43.61$, $P<0.001$; Short vs Long, $F_{1,11}=0.57$). (2) In the 500–1000 ms following

Fig. 3 Contingent negative variation of 12 subjects over the supplementary motor area (*SMA*), the primary motor area (*MI*), and the upper part of the parietal area (*PAR*) in conditions Short (*S*), Long (*L*), and Neutral (*N*). *Abscissa* Time elapsed (2 s) from the beginning of the preparatory signal (onset of the recordings) to the beginning of the response signal (*long vertical bar*). *Ordinates* amplitude of the Laplacian (initial *vertical bar* –0.1 μV/cm^2). In the *bottom right*, the *black horizontal bars* represent the lighting of the signals (*PS* preparatory signal, *RS* response signal)



the PS, the effect of conditions ($F_{2,22}$=20.92, P<0.001) became specific of the primed duration: Condition Short produced a larger CNV than condition Long ($F_{1,11}$=5.91; P<0.05) and condition Neutral was again different from the two others (Neutral vs Short, $F_{1,11}$=36.43, P<0.001; Neutral vs Long, $F_{1,11}$=15.47, P<0.01). (3) In the last 300 ms of the PP, the effect of conditions was not significant anymore ($F_{2,22}$=2.51).

Over MI, the CNVs corresponding to the different priming conditions overlapped in the major part of the PP, as shown by Fig. 3. The effect of conditions became significant ($F_{2,22}$=7.62, P<0.01) in the last 300 ms (thus contrasting with the effect over the SMA). In the last 100 ms, the effect of conditions over MI ($F_{2,22}$=9.72, P<0.01) became specific of the primed duration before the RS: the CNV was larger in condition Short than in condition Long ($F_{1,11}$=6.91, P<0.025) and smaller in condition Neutral than in the two others (Neutral vs Short, $F_{1,11}$=16.04, P<0.01; Neutral vs Long, $F_{1,11}$=5.36, P<0.05).

Note that the sharp notch that can be observed in the middle of the PP over the SMA corresponds to the potential evoked by the extinction of the PS. No noticeable phasic activity was detected by the electrode PAR, although it was closer to the visual areas than is the SMA.

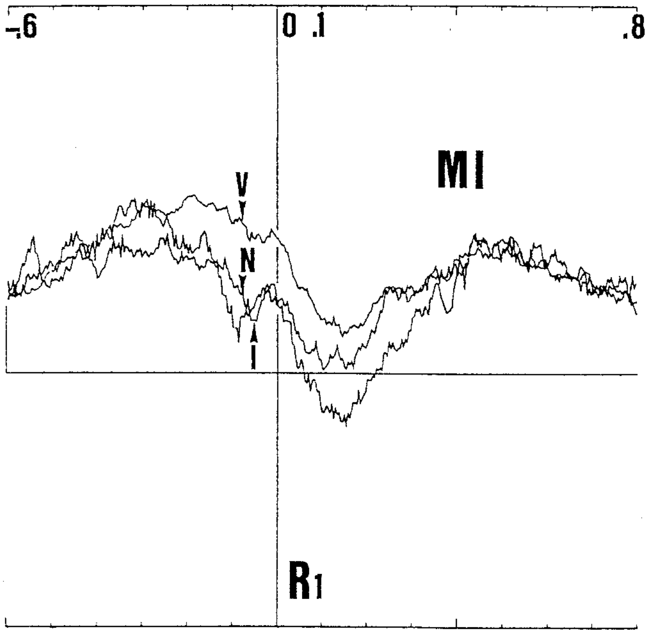


Fig. 4 Electrophysiological activities of 12 subjects obtained over the primary motor area (*MI*) before the first press (*R1*) initiating the response of long duration in conditions Valid (*V*), Invalid (*I*), and Neutral (*N*). Traces are time-locked on R1 and averaged backward. *Abscissa* Time (in seconds). *Ordinate* Amplitude of the Laplacian (initial *vertical bar* –0.1 μV/cm^2). Similar activities were obtained for the response of short duration

Response-related activities

In the following comments, R1 and R2 will designate the first and the second button-presses, respectively, initiating and closing the interval to be estimated. Figures 4 and 5 show the activities time-locked to R1 and R2 in each condition over MI, the only site which yielded a clear effect of the conditions in this backward analysis. Similar traces were obtained whether the R1–R2 interval was long (as illustrated in Figs. 4, 5) or short. A significant effect of conditions ($F_{2,22}$=6.45, P<0.01) was found over MI in the 200 ms before R1 (Fig. 4). The activities

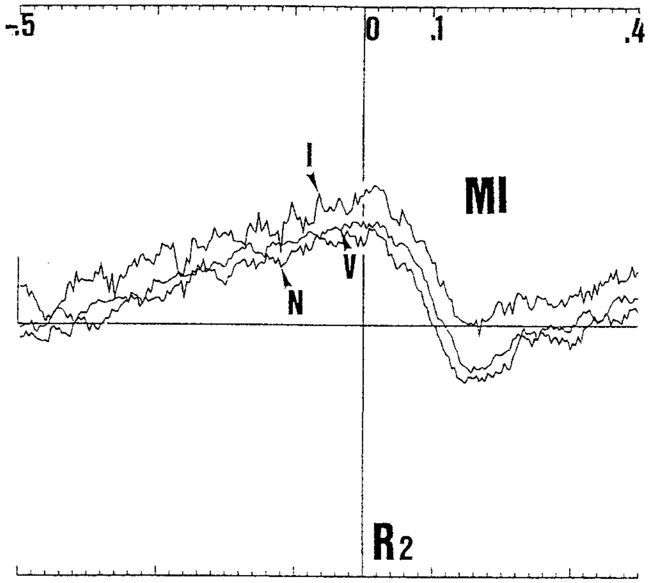


Fig. 5 Electrophysiological activities of 12 subjects obtained over the primary motor area (*MI*) before the second press (*R2*) ending the response of long duration in conditions Valid (*V*), Invalid (*I*), and Neutral (*N*). Traces are time-locked on R2 and averaged backward. *Abscissa* Time (in seconds). *Ordinate* Amplitude of the Laplacian (initial *vertical bar* –0.1 µV/cm²). Similar activities were obtained for the response of short duration

were larger under condition Valid than under conditions Invalid or Neutral ($F_{1,11}$=8.38, P<0.025 and $F_{1,11}$=15.16, P<0.01, respectively). Conditions Invalid and Neutral did not differ ($F_{1,11}$=0.58). Note that the amplitude levels were identical under conditions Invalid and Valid until about 250 ms before the voluntary response, i.e., shortly after the subjects had been informed that the prepared duration was not the duration to be produced. Before R2 (Fig. 5), MI was not sensitive any more to the priming conditions. The results were different over the SMA. Clear effects appeared over this area, as illustrated in the upper part of Fig. 6, which presents the R2-related activities in each condition when the response was short. Condition Invalid yielded the largest activity before R2 and this was greater than that observed in condition Valid ($F_{1,11}$=7.00, P<0.025). The difference between conditions Invalid and Neutral was close to the 0.05 level of significance: ($F_{1,11}$=4.46, 0.05<P<0.1) and there was no difference between conditions Valid and Neutral ($F_{1,11}$=3.56). This effect was limited to the short responses: the corresponding R2-related activities over the SMA when the response was long (Fig. 6, lower part) exhibited no significant difference as a function of conditions ($F_{1,11}$=1.52).

When the activity before R2 was examined over a longer time course, a progressive increase in negativity was detected over MI but not over the SMA. Figure 7 presents the Laplacian changes time-locked to R2 and averaged backward over the SMA and MI in the 2.5 s responses under condition Valid. The component which develops over MI was interpreted as a Bereitschaftspotential (BP) induced by the self-triggered response. It was particularly clear in the responses of long duration (when the responses were of short duration, the post-R1 and pre-R2 activities overlapped).

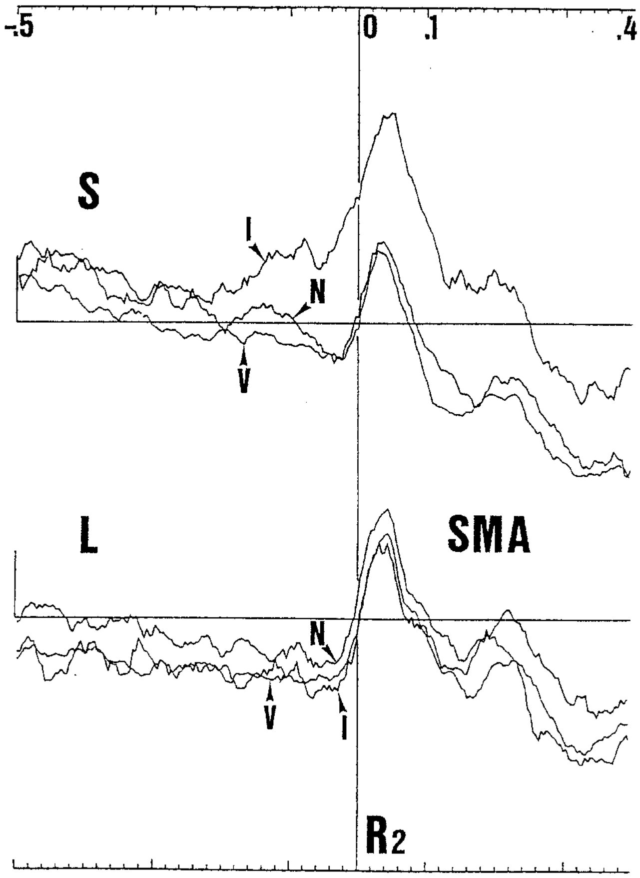


Fig. 6 Electrophysiological activities of 12 subjects obtained over the supplementary motor area (*SMA*) before the second press (*R2*) ending the response of short (*top*) and long (*bottom*) duration in conditions Valid (*V*), Invalid (*I*), and Neutral (*N*). Traces are time-locked on R2 and averaged backward. *Abscissa* Time (in seconds). *Ordinate* Amplitude of the Laplacian (initial *vertical bar* –0.1 µV/cm²)

Late components of the potentials evoked by the RS

Figure 8 presents the activities over the SMA and MI during the 600 ms following the RS, under each condition of information. Over the SMA, a Laplacian change of negative polarity peaked about 220 ms after the RS and was followed by a positive wave peaking at about 320 ms. These waves probably correspond to a N2-P3a complex. They appeared with a particularly large amplitude under condition Invalid. MI yielded no N2-P3a complex, but only a P3 component whose amplitude increased with the probability of occurrence of the conditions (as also seen with N2 over the SMA). Similar (though weaker) effects of the probability appeared on P3 over the parietal site.

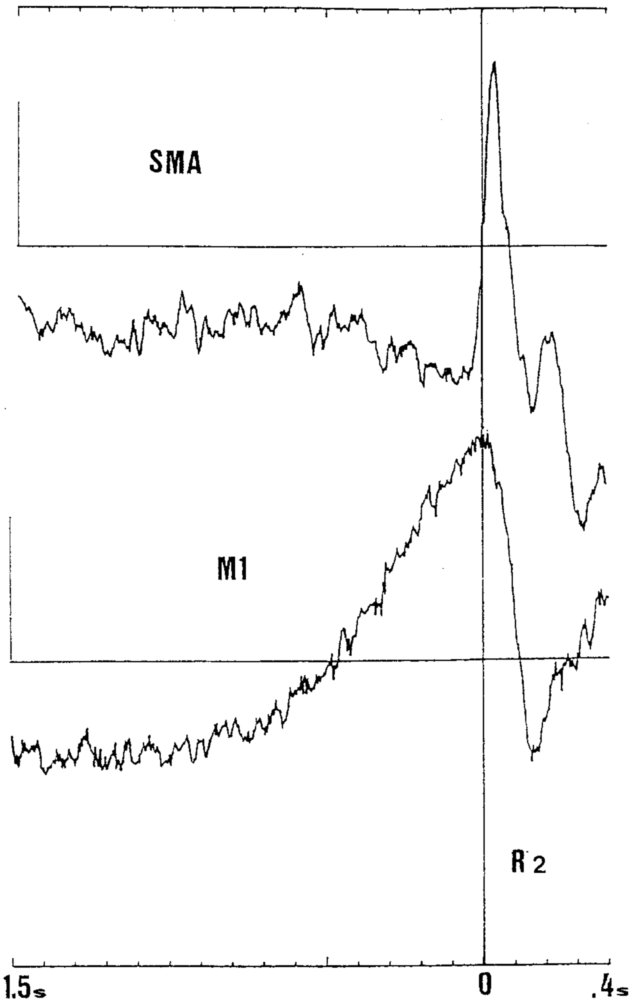


Fig. 7 Electrophysiological activities of 12 subjects obtained in condition Valid over the supplementary motor area (*SMA*) and the primary motor area (*MI*) before the second press (*R2*) ending the response of long duration. Traces are time-locked on R2 and averaged backward. *Abscissa* Time (in seconds). *Ordinate* Amplitude of the Laplacian (initial *vertical bar* –0.1 µV/cm²)

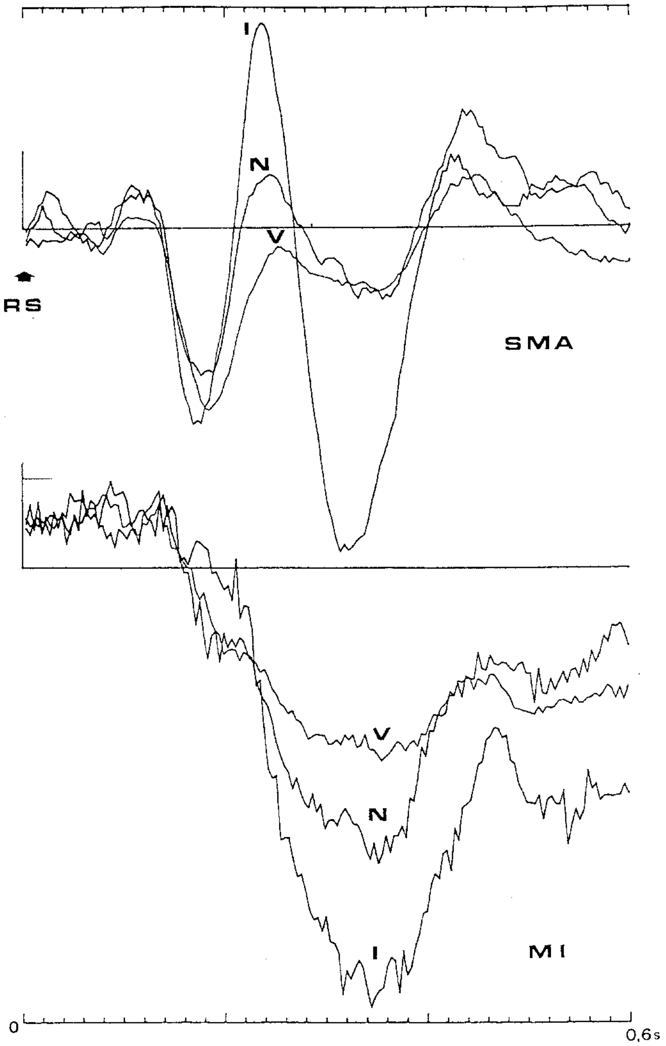


Fig. 8 Evoked potentials of 12 subjects obtained over the supplementary motor area (*SMA*) and the primary motor area (*MI*) after the response signal (*RS*) in conditions Valid (*V*), Invalid (*I*), and Neutral (*N*) when the response was of long duration. *Abscissa* Time (in seconds). *Ordinate* Amplitude of the Laplacian (initial *vertical bar* –0.1 µV/cm²). Similar activities were obtained for the response of short duration

Discussion

RT: behavioral evidence for the programming of duration

The decrease in RT as a function of the probability of the RS (condition Valid 0.81, condition Neutral 0.50, condition Invalid 0.19) is in accord with uncertainty effects, and, hence, cannot be interpreted as revealing programming operations. In contrast, the fact that RTs were shorter before the 0.7-s interval than the 2.5-s one under conditions Neutral and Invalid, whereas no such a difference appeared under condition Valid, confirms the data obtained by Klapp et al. (1974) with very brief durations and by Vidal et al. (1991) with longer ones. As argued in the Introduction, this "short-long" effect suggests that the interval duration was specified as a parameter of the motor program. The effect cannot be attributed to a speed-accuracy trade-off, since the accuracy indices did not vary as a function of the conditions of information or of the interval durations.

The data obtained under condition Invalid were somewhat surprising. The short-long difference under conditions Invalid and Neutral was nearly identical, 13 and 14 ms, respectively. This suggests that the programming operations which preceded response execution did not differ between these conditions. Moreover, the mean difference in RT between conditions Invalid and Neutral (15 ms) was surprisingly small compared with the difference between conditions Valid and Neutral (36 ms): such a small difference would mainly reflect effects of uncertainty or response selection rather than motor effects. Thus, the data obtained under condition Invalid did not conform to predictions: the RT did not reflect the cost of deprogramming operations, even though the RS contradicted the PS. It appears that the deprogramming operations involve no cost, are absent, or are postponed until after the response.

Electrophysiological evidence for the programming of duration

CNV during the PP

The parietal area showed no variation across the present conditions, perhaps because temporal rather than spatial parameters were relevant. Various interpretations can be proposed for the differences in CNV amplitude over the SMA that appeared 300–500 ms after the PS. These differences may be related to programming operations, but, alternatively, they may reflect the different levels of information delivered by the PS under conditions Short and Long compared with condition Neutral. The latter interpretation cannot apply to the effects observed 500–1000 ms after the PS. Here, CNV differences between conditions Short and Long point to temporal specificity: the level of brain activity depended on the duration of the prepared response. The fact that this level of activity was different before a 0.7- and a 2.5-s response is consistent with the differences observed in RT and suggests that the two response durations were specified by distinct programs. These data confirm that certain parameters of a response can be programmed as soon as the relevant information is available, i.e., during a PP initiated by an informative precue. The data indicate that duration itself can be controlled and programmed before execution (and thus is a relevant parameter in the motor program) and that the SMA is involved in duration programming. This conclusion probably holds whatever the mechanical characteristics of the response, since the effects reported here with interval production are similar to those observed by Macar et al. (1990) when the duration was produced by a continuous button-press. The role of the SMA in timing is sustained by neuropsychological evidence (Halsband et al. 1993): unilateral lesions including the right SMA provoke severe bilateral alteration of timing ability in humans.

Over MI, the effect of the priming conditions was detected only at the end of the PP, that is when this effect was not significant anymore over the SMA. Such a tradeoff in the activities of those two areas suggests that information was transfered from the SMA to MI. This result may indicate that the SMA is less a "supplementary" than a "supra" motor area, contrary to the opinion promoted by Chen et al. (1991).

These conclusions rest on the assumption that the Laplacian obtained over the SMA reflects activation of this structure. A major part of the SMA lies deep in the interhemispheric fissure, and deep sources do not produce measurable Laplacians (Nuñez 1981). However, Braak (1980) identifies a zone of the first frontal circonvolution, in humans, which he refers to as the "superofrontal magnopyramidal region" (SMR). He considers that the area activated by speech tasks in the experiments of Larsen et al. (1978) corresponds to this SMR. Now, Larsen et al. (1978) indicate that the involvement of the superofrontal area in their speech task reveals SMA activation. This opinion is supported by the fact that the same part of the superofrontal area was activated by the execution or the mental simulation of a complex motor sequence (Roland et al. 1980). The SMR extends in the interhemispheric fissure but also covers a superficial zone outside this fissure, in the most superior part of the first frontal circonvolution. Therefore, we assume that the activities that were available to the source derivation method were generated by a most superficial, extrafissural, part of the SMA.

Is it possible that what we have called SMA activity includes contamination from other areas? Let us examine the potential candidates: (1) On the caudal part lies the MI of the inferior limbs. Its involvement in the task is not plausible. (2) Below the SMA is the rostral cingular area. It is unlikely to influence our recordings, because, as mentionned earlier, deep sources do not produce measurable Laplacians. (3) The lateral sides correspond to the lateral premotor areas. If they were involved, the effects observed over the SMA should also appear over MI, since premotor areas are as close to MI as to SMA. (4) The prefrontal areas do not seem to be responsible for the present data either. In a task similar to the one used here, Macar et al. (1990) observed activation of the SMA but not of prefrontal areas (lead placed over F3). (5) Finally, the observed activity could be due to the mesial part of the prefrontal cortex, rostral to the SMA. However, the equivalent dipoles in that area are tangentials, deep and remote. Hence, their contribution to the activity calculated over the SMA should probably be modest. In any case, the anterior borders of the SMA are ill-defined. In conclusion, it seems reasonable to consider that the activities that we recorded at FCz originate mainly from the SMA.

Our data can be compared with those obtained by MacKay and Bonnet (1990) in humans. In a precueing task involving forearm movements, the MI and the SMA were most influenced by the precueing of the force and of the direction, respectively. The SMA, though active, was not differentially affected by the precueing of those parameters. This suggests that the SMA, though involved in programming processes, is not concerned with the programming of force or direction. (Relative changes in activity localized in particular brain areas as a result of the manipulation of experimental parameters probably provide more information than relative amounts of activity between areas. As an example, if only CNV amplitudes obtained at the end of the PP had been compared here, the SMA and MI would have appeared as equally involved in duration programming and as working in parallel. In contrast, the different sensitivity of these areas to precueing conditions at different moments of the PP pointed out sequential processes.) Our data indicate, conversely, that the SMA is involved in the processing of the duration of the response. The fact that different cortical areas appear to be devoted to the programming of certain parameters but not of others is an additional argument in favor of the parametric conception of motor programming.

However, van Boxtel et al. (1993) found larger CNVs when no precue was available. In our opinion, this result reflected changes in the subject's arousal level. In contrast with what was done in our experiment, these authors used strong constraints on RT: trials where RT was longer than 400 ms were rejected. This period was perhaps sufficient to perform the mental operations required in the precued conditions but not when no precue was available, unless the subjects increased their arousal level. This interpretation is supported by the fact that the CNV becomes larger when the temporal constraint increases (Otten et al. 1995).

"No go" potentials

After the RS, MI and the parietal site yielded a classic P3 component whose amplitude was inversely related to the probability of occurrence of the different conditions. Over the SMA, a negative-positive biphasic complex was identified. This complex was of very large amplitude under condition Invalid. This large activity under condition Invalid seems to reflect motor inhibition of the previously prepared "wrong" response. This conclusion fits with the data of Gemba et al. (1990), who recorded the corticogram of monkeys in a "go no-go" task. The animals had to give a motor response to a signal and no response to another one. A negative potential was observed in the no-go condition and was interpreted as the electrical sign of motor inhibition.

However, the shape, the topography, and the latency of this complex rather leads to consider it as a N2-P3a wave. In order to evaluate the temporal relationship between this N2-P3a and the onset of the motor command, we measured a posteriori the EMG onset in two subjects submitted to the priming task. The delay between the EMG onset of the first interosseous dorsalis and the RT was 50 ms on average. Magnetic transcranial stimulation enables one to measure conduction time between cortex and muscles: 19.5 ms (Toleikis et al. 1991) and 20.5 ms (Fuhr et al. 1991) for different finger muscles. Hence, the time elapsed between the onset of the motor command and the RT can be estimated to be around 70 ms. Under condition Valid, the RT was about 250 ms. Therefore, the motor command should originate in the motor cortex about 180 ms after the RS. The potentials obtained under conditions Valid and Invalid began to differ 180 ms after the RS. These temporal relationships suggest that the N2-P3a observed here under condition Invalid reveals the inhibition imposed on MI by the SMA. In other words, the SMA seems to withhold the wrong program. Despite the typical interpretation of the N2-P3a complex as a perceptual index, it seems to be related, here, to motor inhibition. If the above interpretation is correct, it implies that, depending on the circumstances, the N2-P3a complex is related to perceptual or to motor processes. The function subserved by the N2-P3a might depend upon the particular structure which generates it and which is possibly different according to the task. This view might even be extended to most Event Related Potentials (ERPs) and is similar to that of Halgren on the P3: "It might be more accurate to think of the P3 as representing a *mode* of information processing extending across many cortical and subcortical regions rather than as the activation ... or ... deactivation of a single region." (Halgren 1988, p. 385). Such considerations should promote extensive use of topographical methods in the study of ERPs.

Programming and deprogramming time courses

The cortical activities preceding R1 and R2 can be summarized as follows: MI yielded differential activity as a function of the priming conditions before R1 but not before R2. The SMA yielded no difference before R1 but presented greater activity under the Invalid condition before R2 when the response was of short duration.

Over MI, the pattern of activities suggests, as expected, that the programming of duration was achieved before R1 and thus did not take place during response execution. However, a different conclusion is reached as concerns deprogramming operations. Indeed, conditions Invalid and Neutral produced very similar effects before R1. This result seems to be the electrophysiological counterpart of the unexpected similarity found between these two conditions on the basis of the RT data. It reinforces the idea that very similar operations were performed under both conditions. The common operations needed consisted of programming the duration cued by the RS. As already discussed, no additional deprogramming operation concerning the wrong duration primed under the Invalid condition seems to have occurred before R1.

Is it then possible to argue that deprogramming occurred during response execution? In the responses of short duration, the large negativity found under condition Invalid over the SMA supports this hypothesis. A tentative interpretation of this activity is that it reflected the late erasing of the wrong program (concerned with the long duration). In the trials where a long duration had to be produced after a short one had been primed, the cortical index of the deprogramming operation was probably "diluted" during the long execution period and, hence, could not be detected after averaging.

No BP over the SMA?

A final question concerns the BP yielded by the sequential button-presses involved in the timing task. The 2.5-s responses were of sufficient duration to enable the detection of a BP over MI, free from the contamination of the motor potentials evoked by the execution of R1. The absence of BP before R2 over the SMA is at variance with

Table 1 SMA activity observed with topographical methods during motor tasks in humans. (*MEG* magnetoencephalography, *EEG* electroencephaalography, *MRI* magnetic resonance imaging)

Reference	Method	Task	SMA activity
Neshige et al. (1988)	Subdural recordings	Finger lifting	Weak and late
Cheyne and Weinberg (1989)	MEG	Finger lifting	No
Kristeva et al. (1991)	MEG	Finger lifting	No
Bötzel et al. (1993)	EEG: dipole localization method	Finger lifting	No
Kim et al. (1993)	Functional MRI	Simple repetitive finger movements	No
Colebach et al. (1991)	Regional cerebral blood flow	Simple timed movements	Yes
Roland et al. (1980)	Regional cerebral blood flow	Simple repetitive finger movements	No
		Isometric finger contraction	No
		Complex sequential finger movements	Yes
		Idea of complex sequential finger movements	Yes
Lang et al. (1990)	EEG: scalp current density	Finger tapping	Yes
Ikeda et al. (1992)	Subdural recordings	Finger lifting	Yes
Rao et al. (1993)	Functional MRI	Simple repetitive finger movements	No
		Complex sequential finger movements	Yes
		Idea of complex sequential finger movement	Yes

the usual opinion that the BP, which characterizes voluntary self-paced movements, begins in the SMA and ends with the later activation of MI (Deecke and Kornhuber 1978).

However, the absence of SMA activity in voluntary self-paced movements has been noticed on several occasions. Table 1 presents recent results obtained by authors who used a topographical method during a motor task performed in humans. First, it is clear that the SMA is not systematically activated in self-paced movements; second, it is not a matter of method, as suggested by Cheyne and Weinberg (1989). Rather, Table 1 suggests that SMA activation is a matter of task. Except in the case of one patient recorded by Ikeda et al. (1992), the SMA does not seem to be significantly involved when the response is simple (the "simple" responses studied by Colebatch and al. 1991, were timed by a metronome and seem closer to a tapping task than to simple repetitive responses). On the contrary, the SMA is activated when the response is complex (as are sequential movements) or, rather, when the complexity of the program requires controlled selection, since the mental representation of sequential finger movements does activate the SMA in the absence of an overt motor response (Roland et al. 1980; Rao et al. 1993). This view has been put forward by several authors (Porter 1990; Deecke 1990); Wiesendanger (1986) proposed that "... the SMA is involved only if the voluntary movements demand conscious attention, not if they are performed automatically." In our experiment, the absence of SMA involvement before R2 might thus be due to the fact that response programming was completed before R1 and that only automatized processes underlying the execution of the sequence took place thereafter.

Conclusion

The present study provided behavioral and electrophysiological evidence for programming processes in a priming paradigm where duration was the parameter to be controlled. Indices of deprogramming operations probably occurred during the execution of the response, but could not be detected before it. MI seemed to be sensitive to programming processes later than the SMA, whose inhibitory function in motor control was suggested by the electrophysiological data.

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