Response Competition in the Primary Motor Cortex: Corticospinal Excitability Reflects Response Replacement During Simple Decisions

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Departments of Physiology and Stomatology, Medicine Dentaire, and Groupe de recherche sur le système nerveux central, Département de Physiologie, Université de Montréal, Montréal, Québec, Canada; and Department of Neurology and Neurosurgery, Montréal Neurological Institute, McGill University, Montréal, Québec, Canada

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Michelet T, Duncan G, Cisek P. Response competition in the primary motor cortex: Corticospinal excitability reflects response replacement during simple decisions. J Neurophysiol 104: 119–127, 2010. First published May 5, 2010; doi:10.1152/jn.00819.2009. It has been suggested that, during decisions about actions, multiple options are initially specified in parallel and then gradually eliminated in a competition for overt execution. To further test this hypothesis, we studied the modulation of human corticospinal excitability during the reaction time of the Eriksen flanker task. In the task, subjects responded with finger flexion or extension to a central arrow while ignoring congruent or incongruent flanker arrows. Single-pulse transcranial magnetic stimulation (TMS) was applied over primary motor cortex (M1) at one of five different latencies after stimulus onset, and motor-evoked potentials (MEPs) were measured in the contralateral index finger. During the control (no flankers) and congruent conditions, MEP size in the agonist increased gradually over the course of reaction time, indicating an increase in corticospinal excitability. Conversely, when the same muscle acted as an antagonist, MEP size decreased, suggesting inhibition. Critically, in the incongruent condition, MEPs briefly increased in the muscle corresponding to an initial default response to the flanker arrows and were later replaced by MEPs corresponding to the correct response to the central arrow. Finally, we found that the gradually growing MEPs for the three conditions reached a constant maximum level just before movement initiation. We propose that this dynamic modulation in corticospinal excitability reflects the competition process, leading to the selection of one response and the rejection of the other. Our results suggest that response competition influences activity in primary motor cortex and that its timing directly influences motor output latency.

INTRODUCTION

Recent neurophysiological studies have suggested that decisions about actions involve many of the same brain regions implicated in the planning and execution of movements (Cisek and Kalaska 2005; Glimcher 2003; Gold and Shadlen 2007). These observations have motivated the hypothesis that decisions about actions are made through a biased competition between representations of the potential actions (or affordances) (Cisek 2006, 2007), analogous to the mechanism believed to underlie selective attention (Desimone and Duncan 1995). According to this model (Erlhagen and Schöner 2002; Furman and Wang 2008; Tipper et al. 2000), sensory information is used to specify potential actions as regions of activity in a distributed population of directionally tuned cells. Distinct actions produce distinct hills of activity, which compete against each other through lateral inhibition (Sherrington 1906). This competition is biased by influences from a variety of sources, including prefrontal cortex (Hoshi et al. 2000; Kim and Shadlen 1999) and the basal ganglia (Redgrave et al. 1999), and the system commits to a given choice when the activity associated with that choice reaches a fixed threshold (Gold and Shadlen 2007).

One important prediction of the affordance-competition hypothesis is that neural correlates of decisions should be present even at relatively late stages of processing, possibly even in M1. Here, we study this prediction by measuring corticospinal excitability (CSE) while human subjects perform a simple response-selection task. We used single-pulse transcranial magnetic stimulation (TMS) over M1 to determine CSE by measuring the motor-evoked potentials (MEPs) in contralateral muscles. Previous studies have shown that CSE is modulated as subjects prepare to execute movements. Using TMS in different bi-manual experimental paradigms (self-paced movement, go/no-go, choice reaction time, etc.), some authors (Chen and Hallett 1999; Leocani et al. 2000) found a gradual facilitation of the agonist muscle, beginning ~80–120 ms before movement, in a manner reminiscent of the build-up activity observed in single-unit recording studies (Lebedev et al. 2008; Roux et al. 2006). Therefore if neural activity in M1 reflects aspects of a competition between potential actions, changes in CSE should show the time course of that competition.

We used a modified version of the Eriksen flanker task, a well-known paradigm for studying response conflict (Fig. 1 and METHODS) (Botvinick et al. 1999; Eriksen and Eriksen 1974). Using this task, EEG experiments have shown that irrelevant stimuli are processed throughout the sensorimotor system (Coles et al. 1985, 1988; Eriksen et al. 1985; Mattler 2003; Smid et al. 1990). However, the low spatial resolution of EEG does not allow one to establish whether this processing...
extends into the groups of neurons that specifically control the muscles involved in the response. Here, we use TMS to test this and predict that CSE will show the time course of response preparation during the task and reflect not just the choice that is made but also its timing. Some of these results have been previously presented in abstract form (Michelet et al. 2008).

METHODS

Participants

Ten right-handed subjects (4 women; age, 24–38 yr) with normal or corrected-to-normal vision participated in the experiment. The experimental procedure was approved by the local ethics committee, and all subjects gave written informed consent before the experiment. One subject reported repeated problems of vigilance during the task and was discarded from the analysis.

Task design

The subjects performed the Eriksen flanker task (Botvinick et al. 1999; Eriksen and Eriksen 1974), responding by either flexing or extending the index finger of their right hand to the appearance of a visual stimulus. Participants were seated in a comfortable chair, 1.1 m from a computer monitor. Their wrist was constrained during the experiment, and subjects were specifically instructed to perform the task only with their right index finger without moving any other joints. A custom-built apparatus supported the right forearm and hand. It was equipped with an infrared position sensor at the central (rest) position of the index finger and left and right peripheral buttons with adjustable distance from the center (Fig. 1A). This allowed the detection of both the finger release from the rest position and the actual choice (button pressed) made by the subject. The task is an arrow version of the classical Eriksen flanker task (Fig. 1B). Three different conditions were used in the task. In the control condition, a single arrow (→ or ←) appeared on the screen, and subjects were asked to flex if it pointed to the left or extend if it pointed to the right. In the congruent condition, four additional flanker arrows appeared beside the central arrow, pointing in the same direction (↔ ↔ ↔ ↔ or → → → →). In the incongruent condition, the flanker arrows pointed in the opposite direction and the subject was instructed to respond only on the basis of the central arrow (flexion for → → → → and extension for ← ← ← ←). All stimuli were presented in white on a black background. The relative proportion of congruent, incongruent, and control trials were, respectively, 40, 40, and 20% of the total number of trials. Each trial began with a 500 ms warning symbol (*) displayed at the center of the screen, followed by a 300 ms delay, which preceded the presentation of the cue arrow(s). The subject had 2,000 ms in which to respond. Visual feedback (500 ms duration, “Correct” written in green for a correct trial and “Wrong” written in red for an incorrect trial) was provided 600 ms after the movement was completed. Cue arrows were displayed until the movement onset.

EMG and MEP recording

Surface electromyographic recording was performed in the first dorsal interosseus muscle (FDI, a finger flexor) and over the extensor indicis muscle (EI) of the right hand. EMG activity was amplified (×1,000 to ×5,000), band-pass filtered (100 Hz to 3 kHz), digitized on-line (rate 4 kHz), and later rectified and integrated. The detection of movement onset for flexion (leftward movement) and extension (rightward movement) was determined as the voluntary contraction onset of FDI and EI muscles, respectively, using MATLAB programming and verified visually for each trial (Fig. 1C). Because EI is a deep muscle, electrodes over EI recorded not only extensor activity but also flexor activity. Nevertheless, it allowed us to properly detect the extension onset, as verified by systematic comparison with the position sensor onset time. Indeed, although pure flexion involved both FDI and EI activity, extension involved only EI contraction. Thus our analyses of MEPs focused on the FDI muscle, and flexion and extension are referred to in the RESULTS and DISCUSSION as agonist and antagonist movements, respectively.

TMS testing

A figure-of-eight coil (Double 70 mm Coil, Magstim, Whitland, UK) was used to stimulate M1 over the left hemisphere. The coil was connected to a Magstim stimulator (Magstim Super Rapid, maximum output 2 T, Magstim) and was held tangentially on the left hemiscalp with its handle pointing backward at an angle of ~45° from the mid sagittal axis. The motor hotspot was defined as the optimal (minimum TMS intensity) position for induction of MEPs of ~1 mV peak-to-peak amplitude at rest. Throughout the experiment, the coil was manually maintained over the hotspot using the Brainstim
frameless stereotaxy system (RogueResearch, Montreal, Canada) to continuously monitor coil placement. The MEP produced by the stimulation was measured from the FDI muscle of the right hand. (As previously mentioned, it was not possible to analyze exclusively the IE MEPs because of contaminating flexor activity.) The size of this MEP (peak-to-peak amplitude measure) was used as a measure of the corticospinal excitability at the time of the TMS pulse (Fig. 1C).

The experimental design was divided into five blocks of 100 trials. After verbal explanation of the task and a few preliminary trials (<10), each experiment started with a practice block of 100 trials without stimulation to evaluate EMG activity, reaction times (RTs), and error rates without TMS interferences (No TMS trials). During the remaining four blocks, TMS was applied for each trial (TMS trial), with a 6.7 ± 0.3-s interstimulus interval. The TMS pulse was applied over left primary motor cortex at one of five different latencies (t1–t5) after cue onset (80, 160, 240, 320, and 400 ms, respectively). The three trial conditions, the two movement directions, and the five stimulation times were interleaved in a pseudorandom order, and the mean number of MEPs computed for each of the 30 different experimental conditions was 12.5 per subject. The same 500-trial sequence was presented to each subject. For 8 of 10 subjects, we also performed conditions was 12.5 per subject. The same 500-trial sequence was presented to each subject. For 8 of 10 subjects, we also performed conditions was 12.5 per subject. The same 500-trial sequence was presented to each subject. For 8 of 10 subjects, we also performed conditions was 12.5 per subject. The same 500-trial sequence was presented to each subject. For 8 of 10 subjects, we also performed conditions was 12.5 per subject. The same 500-trial sequence was presented to each subject. For 8 of 10 subjects, we also performed conditions was 12.5 per subject. The same 500-trial sequence was presented to each subject. For 8 of 10 subjects, we also performed conditions was 12.5 per subject. The same 500-trial sequence was presented to each subject. For 8 of 10 subjects, we also performed conditions was 12.5 per subject. The same 500-trial sequence was presented to each subject. For 8 of 10 subjects, we also performed conditions was 12.5 per subject. The same 500-trial sequence was presented to each subject. For 8 of 10 subjects, we also performed conditions was 12.5 per subject. The same 500-trial sequence was presented to each subject. For 8 of 10 subjects, we also performed conditions was 12.5 per subject. The same 500-trial sequence was presented to each subject. For 8 of 10 subjects, we also performed

### Behavioral measures

The RT was measured between the cue appearance and the beginning of the voluntary change in EMG activity (Fig. 1B). RTs > 1,000 ms were considered to be incorrect responses. For the statistical analysis of RTs, three factors were considered: task conditions (control, congruent, or incongruent), stimulation time (no TMS or TMS at t1–t5), and muscle involved (agonist or antagonist). ANOVAs and t-test with Bonferroni-Dunn correction for post hoc analysis were used. We set the significance levels for the ANOVAs to P < 0.01 to correct for multiple comparisons and for the post hoc t-test to P < 0.05. All data are given as means ± SE.

### Behavioral results

We first performed a one-way ANOVA on RTs recorded in no-TMS trials in both agonist and antagonist movements. This showed a clear influence of task condition on RT for all subjects [F(2,16) = 134.22; P < 0.0001]. This was confirmed by post hoc comparison, which showed that RTs, expressed in milliseconds, were significantly longer in the incongruent condition (405.2 ms) than in the congruent (359.9 ms) and control conditions (362.6 ms; P < 0.0001). The slight difference between control and congruent condition was not significant (Fig. 2A). The clear separation in RT distribution between these conditions (Fig. 2, B and C) also confirms that this task is well suited to assess the time course of information processing by comparing MEP amplitude among the different conditions. Next, we made a systematic comparison of RTs in flexion and in extension, which indicated an absence of effect (t-test, P > 0.05) for movement direction. Finally, we studied the effect of TMS pulse on RTs. We found that TMS significantly reduced the RTs, and the effect of TMS on RTs was stronger when the pulse was delivered earlier (paired t-test; see Fig. 2D: *P < 0.05; **P < 0.01; ***P < 0.001). Errors were rare (<3%) and only present in the incongruent condition.

### MEP data

The mean intensity of a single TMS pulse needed to evoke an MEP of ~1 mV at rest was 63.3 ± 6.8% of the stimulator output. MEP amplitude was examined within a 29.8 ± 1.8 ms epoch beginning 20.2 ± 1.8 ms after the TMS pulse (epochs were chosen after individual examination of MEPs for each subject). The mean MEP amplitude at t1 for the six conditions (congruent agonist, incongruent agonist, control agonist, congruent antagonist, incongruent antagonist, and control antagonist) were 1.07, 0.83, 0.87, 1.01, 0.97, and 1.15 mV, respectively [ANOVA, main effect of condition: F(5,370) = 1.01; P = 0.42]. Figure 1C shows an example of typical EMG activity recorded from the FDI before, during, and after the TMS pulse.

Figure 3 shows the relative MEP amplitude for each stimulation time. Statistics described below refer to results for all subjects, represented in Fig. 3B. Using a paired t-test, we systematically compared agonist and antagonist MEP amplitudes for a given TMS time to find the time at which the CSE reflected information on motor preparation. In control and congruent trials, cortical excitability gradually increased during agonist movements and decreased during antagonist movements. The difference between MEPs in agonist and antagonist movements became significant at t3 (time = 240 ms; t-test, P < 0.0001).

In contrast to the control and congruent trials, in the incongruent condition, CSE exhibited correlates of response replacement. In particular, FDI excitability was larger for antagonist movements when the TMS pulse was delivered early (<240 ms; t-test, P < 0.0001) but larger for agonist movements when the TMS was delivered late (>240 ms, t-test, P < 0.0001).
For each subject, we estimated the timing of response replacement by interpolating the time course of corticospinal excitability with a cubic spline and finding the “crossing time” at which the CSE for extension trials fell below the CSE for flexion trials (Fig. 4A). We compared each subject’s “crossing time” from incongruent trials with that subject’s mean RTs in control, congruent, and incongruent conditions. We found a significant and monotonic relationship whereby subjects with fast crossing times tended to have the fastest RTs (Fig. 4B). In other words, subjects who were fast at response replacement during incongruent trials were also fast at initiating their movements in all task conditions.

We examined precisely whether MEP amplitude could allow us to predict the RT for each trial (Fig. 4, C and D). We compared MEP amplitude as a function of TMS time normalized by each trial’s RT. This “TMS-time/RT ratio” formalized the relative time from the TMS pulse to the movement onset, such that 0 represents stimulation at cue onset time and 1 represents stimulation exactly at the movement onset time. We found a gradual increase in MEP amplitude as this ratio approached 0.8 (Fig. 4D). At this point, MEP amplitude reaches a maximum value (mean, 0.65). Interestingly, this maximum was virtually identical for the three conditions, preceded the movement onset at fixed latency, and was followed by a decrease in amplitude as the ratio approached 1. This suggests that a movement was initiated when the corticospinal excitability reached a constant threshold.

**DISCUSSION**

A number of theories have suggested that the sensorimotor system can simultaneously encode multiple potential actions that compete for overt execution. For example, according to the continuous flow model (Coles et al. 1985) any information in stimulus array associated with a response channel will activate that channel; and 2) if a particular array contains information that activates two different response channels, the concurrent activation of these channels will produce mutual inhibition (Smid et al. 1990). Likewise, the “affordance competition hypothesis” (Cisek 2006, 2007) suggests that sensory information is used to specify, in parallel, representations of several potential actions. These representations compete through mutual inhibition biased by a variety of influences. Neural studies have shown correlates of multiple potential reaching actions in parietal and premotor cortex (Cisek and Kalaska 2005; Scherberger and Andersen 2007), suggesting that the competition underlying action selection plays out across a large distributed system. The aim of this study was to indirectly test whether this competition can extend into the level of neural activity in primary motor cortex.

The Eriksen flanker task is believed to manipulate competition at the response level (Eriksen and Schultz 1979). As
expected, our behavioral results replicate the classic finding that RTs for incongruent trials are significantly longer than for congruent ones. The increase in RT is believed to result from a competition between mutually exclusive potential responses. Moreover, the clear separation in RT distribution between these conditions (Fig. 2) also confirms that this task is well suited to assess the time course of information processing through comparison of MEP amplitude among the three different conditions.

The primary behavioral effect of TMS is an influence on RTs. Previous studies have suggested that there is an imbalance between an early shortening of RTs caused by intersensory facilitation and a later lengthening as a consequence of an inhibitory process (Ashby et al. 1999; Leocani et al. 2000; Ziemann et al. 1997). As reported in Fig. 2D, our results are in accordance with these studies because TMS significantly modulates the RTs in all task conditions, and we found the "biphasic" pattern of TMS influence on RTs. Importantly, although our TMS focally activates the FDI area, its modulatory effect on RTs occurs in both agonist and antagonist movements. This result allows further comparison of cortical information processing occurring during both flexion and extension movements. Error rate was not increased during TMS trials compared with no-TMS trials and was also equivalent for agonist and antagonist responses. This absence of a difference in error rates favors the interpretation that stimulation did not trigger responses.

When stimulating at different times after presentation of the visual instruction with a fixed TMS output intensity, we found a significant modulation of FDI MEP amplitude during the preparatory period. Our hypothesis suggests that, in control and congruent trials, activity related to the selected action grows over time, causing movement initiation when it reaches a threshold. This is consistent with event related potential (ERP) studies that provided evidence that movement initiation occurred at a certain activation criterion. The P300 latency is considered an index of selective central activation. Its analysis showed that movement initiation is a function of a response activation process controlled by an evaluation process that accumulates evidence gradually (Coles et al. 1985; Smid et al. 1990). Complementarily, lateralized readiness potential (LRP) measures have shown that EMG responses occur when response activation achieves a particular fixed level (fixed amplitude of LRPs at the time of the response onset) (Gratton et al. 1988).

In parallel with the growing agonist activity, our results also showed that activity related to the alternative and antagonist option is gradually inhibited. Hence we predicted a selective increase of MEP amplitude in the muscle used for producing the movement (i.e., the agonist) and a corresponding inhibition of the antagonist (Bogacz et al. 2007; Usher and McClelland 2001). The results shown in Fig. 3 confirm this prediction. We found a significant inhibition in antagonist MEPs in the congruent condition at t3 and t4 and a reversal of antagonist MEP size between t3 and t5 in the incongruent condition. *P < 0.01; **P < 0.001.

**FIG. 3.** Time course of MEP from arrow(s) appearance. A: single-subject result (subject 10) showing that, in the control and congruent conditions, FDI excitability gradually increased during agonist trials and decreased during antagonist trials. In the incongruent condition, FDI excitability was larger for antagonist early in the trial, but larger for agonist later in the trial. B: similar results were found across all subjects with a significant inhibition in antagonist MEPs in the congruent condition at t3 and t4 and a reversal of antagonist MEP size between t3 and t5 in the incongruent condition. *P < 0.01; **P < 0.001.
activity of the antagonist, which supports the inhibition tendency, is not exactly concomitant with the maximum activity of the agonist. This favors the hypothesis that reciprocal inhibition in M1 is also biased and modulated by other influences (Cisek 2006).

During incongruent trials, we predicted that neural activity in M1 first favors the movement direction instructed by the more salient flanker arrows, and later, this “default” response decreases and is replaced by the correct response instructed by the less salient central arrow. The time course of MEP amplitude (Figs. 3 and 4D) supports this prediction. These results complement those obtained by examining EMGs in bimanual tasks, which showed that, in the incompatible condition, EMG activity is evident in both hands (i.e., both in the muscle appropriate to the required response and in the arm muscle related to the incongruent response) (Eriksen et al. 1985). In these cases, RTs are longer than for the congruent stimulus-response association (Eriksen et al. 1985; Hasbroucq et al. 1999). Interestingly, EMG activity for the default, incorrect response always leads the EMG activity for the correct response (Eriksen et al. 1985; Hasbroucq et al. 1999; Rösler and Finger 1993). ERP techniques also provide good evidence of a response competition process through observations that either P300 or LRP in correct and incorrect responses can be activated concurrently on the same trial (Coles et al. 1985, 1988; DeSoto et al. 2001; Valle-Inclán and Redondo 1998).

These results are also consistent with observations of neural activity in the dorsal premotor cortex of the monkey during pro- and anti-reach tasks (Crammond and Kalaska 1994). During anti-reach movements, PMd cells exhibit an initial burst followed by suppression. It has been suggested that the initial burst is the correlate of an initial “default” response to move directly toward the target, followed by a suppression indicating the replacement of the default action with the correct anti-reach action. However, a similar response replacement process was not observed in monkey M1 (Crammond and Kalaska 1994). A plausible reason that no “default” responses were seen in M1 is that the monkeys’ task included an instructed delay during which M1 was suppressed. During a free reaction-time task, such as ours, no M1 suppression is expected, and the competition is more likely to extend into M1. Our results support this prediction. Moreover, the MEP growth for the agonist seems to shift later in time in incongruent trials compared with congruent (Fig. 4C), presumably resulting in

FIG. 4. Behavior/corticospinal excitability (CSE) relationship. A: the crossing time is an estimation of the timing of response replacement during incongruent trials, computed by interpolating and finding the time at which the CSE for antagonist (dotted line) trials fell below the CSE for agonist trials (solid line). This is an example from subject 10. B: the crossing times for each subject were compared with that subject’s mean RTs in control, congruent, and incongruent conditions. C: interpolation of the time course of CSE for agonist and antagonist trials, at each TMS latency, for the 3 conditions (all subjects). D: TMS time/RT ratio is a representation of MEP amplitude as a function of TMS time normalized by each trial’s RT (all subjects).
longer RTs, and there is a monotonic relationship between crossing times and RTs. Both of these results confirm the dependence of motor initiation on M1 excitability.

Because the modulation of MEP amplitude is thought to reflect the dynamic modulation in corticospinal excitability, we propose that these activation/inhibition patterns during incongruent trials provide a measure of the competition between M1 representations of alternative potential actions. Three different possibilities could explain this pattern of activity: cortico-cortical modulation of M1, an effect on spinal motoneurons, or a local process within M1. The former hypothesis is supported by a recent study showing a clear influence, during a conflict condition, of medial frontal cortex on the lateralized readiness potential, a measure of relative level of activity that is indicative of the preparation of the motor response (Taylor et al. 2007). In a study using event-related optical signals (EROSs), DeSoto et al. (2001) provided good evidence that lateralized activity was localized within M1. However, the EROS technique could not show inhibitory processes, and it is possible that response inhibition could explain the existence of a difference in the location of the contralateral and ipsilateral activity observed on incongruent trials (DeSoto et al. 2001).

Moreover, there is a possible contamination of LRP activation recorded over the ipsilateral M1 by ipsilateral parietal activation (Wascher and Wauschkuhn 1996). Importantly, although the P300 provides insightful results regarding response competition processes, it is difficult to distinguish between overlapping components, or sources of these ERPs (see for example Friedman et al. 2001; Frodl-Bauch et al. 1999; Gratton et al. 1992). Most of the experiments studying competition within the motor cortex involved a right or left hand response to the decision cue (Soto et al. 2009). Although there is no obvious reason that neural mechanisms underlying intra- and inter-hemispheric choices should differ, it is nevertheless important to assess response competition at the level of a single effector. In our design, it is physically impossible to simultaneously respond to the cue and the flanks (i.e., performing an index finger extension and flexion at the same time). However, our results suggest that both potential responses can overlap and compete, despite the fact that they are physically mutually exclusive. We believe this goes beyond bimanual studies in which subjects could, at least in theory, perform both a right and left hand movement at the same time (see DeSoto et al.: “when in doubt, do it both ways . . . ”).

Because the results of these studies are concerned with between-hand competition mechanisms (right vs. left movement), their conclusions implicate inter-hemispheric mechanisms. Here, by stimulating the dominant motor cortex when only dominant hand movements were executed, we avoid possible confounds from the nonmoving side and focus on possible interactions between neighboring cells in the left M1. Thus a TMS approach combines the advantages of both high temporal and spatial resolution, allowing us to study the time course of information processing at the level of groups of neurons that specifically command the muscles involved in the response required by the task.

One may argue that the observed modulation of MEP amplitude can be explained by a noncentral effect of TMS. Indeed, we must take into account the possibility that inhibition of MEPs takes place at the spinal level by projection of corticospinal neurons to Ia inhibitory interneurons (Jankowska et al. 1976). In an instructed force production paradigm, Romaiguère et al. (1997) studied the amplitude of the Hoffmann reflex at different times during the RT period to separate the spinal effect of TMS from its cortical effect. The authors reported no detectable effect of electrical stimulation time on the amplitude of the evoked response, favoring the hypothesis that MEP amplitudes reflect mainly the level of CSE at the time of TMS. This result is further confirmed by the finding that, in an RT task, the H reflex increased when the muscle is involved in the response and decreased when it is not, ~35 ms before the muscle contraction (Hasbroucq et al. 2000). The authors also favored the interpretation in which the balance of excitability reflects a property of the central command rather than the spinal circuitry (Hasbroucq et al. 2000). It still remains to be determined whether these activity patterns are a consequence of other cortical influences or a more local process within M1. Although TMS experiments give access to the dynamics of information processing and competition, this technique only addresses population-level activity. It therefore cannot be determined from this study whether this gradual increase of activity results from intrinsic properties of M1 neurons, the influence of other structures on the complete population, or both. It is likely that the summation that occurs during the RT period involves many cortical and subcortical regions projecting into M1. The strong anatomical connection between M1 and PMd areas (Dum and Strick 2005; Takada et al. 2004) and recent findings of their strong functional links favor this hypothesis (Fadiga et al. 2005).

Whatever the cellular bases underlying our results, they suggest that neural activity within the motor system reflects a competition between neural representations of potential actions. Because M1 is thought to implement the final motor output stage, these late activities involved in the response selection process allow relatively late decision-related influences. Because of reciprocal interconnections, the activity of cells anywhere within the system will be related not only to the features of the actions they control but will also reflect the biases for or against a given action in relation to other available options. This result favors the hypothesis that decision-making is not an abstract, purely cognitive process separate from sensorimotor control. At least in cases when decisions are associated with specific actions, decision-making seems to be intimately involved with on-line planning and control of actions, as required by the real-time demands of interactive behavior. Hence the dynamic imbalance between facilitation and inhibition is to be related not only to the selection of an appropriate movement (as provided by reciprocal inhibition at the spinal level) but also to the possibility of adjustment at a relatively late stage of motor execution (Messier and Kalaska 1999). This “high level” ability is in keeping with recent studies showing that M1 is involved in many cognitive processes such as learning, mental imagery or even error observation (Koolewijn et al. 2008; Muellbacher et al. 2001; Tkach et al. 2007).

Finally, one of the most influential models of decision-making is based on the idea that a response is triggered when the signal that represents the decision process reaches a threshold level (Coles et al. 1985; Gold and Shadlen 2007; Gratton et al. 1988; Hanes and Schall 1996; Smid et al. 1990). Albeit cortico-spinal excitability is not a direct measure of neuronal activity, our findings are in good agreement with this model. In
particular, 1) MEP size grows over time, 2) it reaches a fixed level at a fixed latency before the onset of voluntary EMG activity (decision threshold), and 3) the time taken to reach this threshold accounts for much of the variability of RTs.

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**DISCLOSURES**

No conflicts of interest, financial or otherwise, are declared by the author(s).

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