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# Decision making and action implementation: Evidence for an early visually triggered motor activation specific to potential actions

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**Abstract**

To make a decision may rely on accumulating evidence in favor of one alternative until a threshold is reached. Sequential-sampling models differ by the way of accumulating evidence and the link with action implementation. Here, we tested a model's prediction of an early action implementation specific to potential actions. We assessed the dynamics of action implementation in go/no-go and between-hand choice tasks by transcranial magnetic stimulation of the motor cortex (single- or paired-pulse TMS; 3-ms interstimulus interval). Prior to implementation of the selected action, the amplitude of the motor evoked potential first increased whatever the visual stimulus but only for the hand potentially involved in the to-be-produced action. These findings suggest that visual stimuli can trigger an early motor activation specific to potential actions, consistent with race-like models with continuous transmission between decision making and action implementation.

**Descriptors:** Cognition, Normal volunteers, EMG, Decision making, Visual choice, Transcranial magnetic stimulation

## Decision Making and Action Implementation

To make a decision often results in producing a particular behavior. Which basic mechanisms take part in selection among potential actions and implementation of these actions remains to be specified. Many models propose a formalism that specifies the putative basic mechanisms involved in the choice among alternatives based on some feature of a stimulus. Sequential-sampling models can account for both speed and accuracy of performance, as well as prior knowledge and the available sensory information at the moment of the decision (e.g., Gold & Shadlen, 2007). The core assumption in these models is that sensory signals are integrated over time through sequential sampling; the accumulation of evidence in favor of one alternative goes on until it reaches a threshold, leading to the implementation of the selected alternative (e.g., Ratcliff & Smith, 2004).

Sequential-sampling models differ in the way the evidence is accumulated over time (e.g., Smith & Ratcliff, 2004). A common distinction is whether evidence in favor of one alternative is integrated against the other in a single accumulator (diffusion-like models; e.g., Ratcliff & Smith, 2004) or in separate accumulators (race-like models; e.g., Usher & McClelland, 2001). These models also differ by the link between decision making and action implementation, and hence make different predictions on the dynamics of action implementation, as illustrated in Figure 1A. The models with *sequential* transmission predict that action implementation starts only when the accumulation of evidence is complete. In contrast, the models with *continuous* transmission predict that action implementation can start as soon as some evidence is accumulated. Only the race-like models with continuous transmission between decision making and action implementation predict that partial accumulation of evidence in favor of one alternative can directly lead to an early implementation of this alternative. The other models predict that only the selected response is implemented.

In this framework, only the alternatives involved in the choice can be supported by accumulation of evidence. Therefore, any motor activation resulting from the accumulation of evidence is specific to the choice alternatives and hence to the potential actions. The race-like models with continuous transmission thus further predict that the early motor activation is specific to the potential actions. Here, we tested this prediction to specify the mechanisms of decision making and their link with action implementation (Figure 1A). To this end, transcranial magnetic stimulation (TMS) of the motor cortex was used to probe the dynamics of action implementation on the final motor pathway.

## Physiological Evidence for Action Implementation

TMS allows assessment of excitability of the corticospinal pathway as well as of excitatory and inhibitory intracortical circuits within the motor cortex (see Reis et al., 2008, for a review). Pulses passing through a wire coil placed over the scalp induce brief electrical currents in the brain. When applied to the primary motor cortex,

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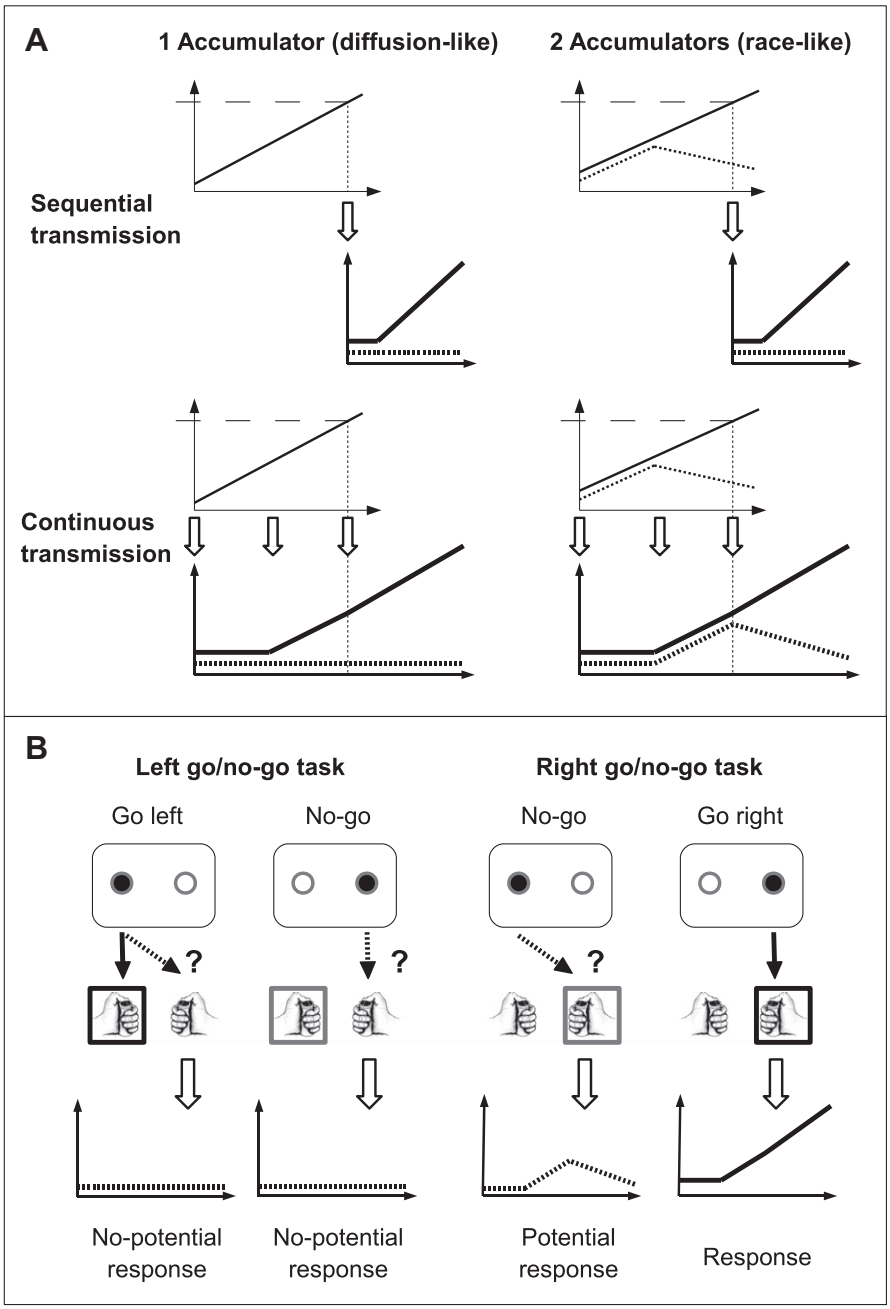


**Figure 1.** A: Illustration of four types of sequential-sampling models that differ by the way the evidence is accumulated: one accumulator (diffusion-like; left column); two accumulators (race-like; right column), and by the link between decision making and action implementation: sequential transmission (upper row); continuous transmission (lower row). For each type, the upper graphic represents the amount of accumulated evidence over time until a threshold is reached (horizontal dashed line), corresponding to the decision-making process; the lower graphic represents the amount of motor activation accumulated over time, corresponding to the action implementation process. The solid line represents the accumulation in favor of the selected response and the dotted line the accumulation in favor of the nonselected alternative. The large white arrows represent the transmission between the decision-making and the action implementation processes. Note that only the race-like model with continuous transmission (lower right) can predict an increase of motor activation for the nonselected alternative. B: Illustration of the displayed stimuli (rectangles with dots, upper row), the to-be-produced responses (hands with buttons, middle row), and the predictions on the motor activation (lower row), for two representative tasks: left go/no-go (left columns); right go/no-go (right columns), and for both go and no-go events. The black dot represents the displayed imperative stimulus; the solid arrows and the black square indicate the response to produce for the go trials. For the no-go trials, the gray square indicates the hand involved in the task. Single-pulse transcranial magnetic stimulation of the left motor cortex was used as an index of action implementation relative to the right stimulated hand. For right go/no-go, the stimulated hand was always the hand involved in the task. For left go/no-go, the stimulated hand was never the hand involved in the task. The line in the graphics (lower rows) represents the expected motor activation over time for the right hand: "Go right" (fourth column, solid line), "Go left" or "No-go" (three first columns, dotted line). Note that the race-like model with continuous transmission predicts an increase of motor activation in the right hand when this hand is a potential response (third column).

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single-pulse TMS can cause a small twitch in the muscle controlled by the stimulated area. The physiological effect of TMS can be quantified by measuring the motor evoked potential (MEP) obtained from surface electromyographic (EMG) activity of the target muscle. The MEP amplitude obtained with single-pulse TMS reflects the net effect of excitatory and inhibitory inputs to the corticospinal pathway. In the paired-pulse TMS paradigm, two separate pulses are delivered to the motor cortex through the same TMS coil (Kujirai et al., 1993). Short interstimulus intervals (ISIs, 2–5 ms) are used to assess short-interval intracortical inhibition (SICI). The first subthreshold (conditioning) pulse is thought to recruit intracortical inhibitory interneurons that reduce the MEP amplitude produced by a second suprathreshold (test) pulse (Di Lazzaro et al., 1998; Kujirai et al., 1993; Nakamura, Kitagawa, Kawaguchi, & Tsuji, 1997).

By delivering TMS to the motor cortex at various times after the occurrence of the imperative stimulus, previous studies provided physiological evidence for an implementation of the selected response. They showed a MEP dissociation between the responding and the nonresponding hands, indicating implementation of the selected response in choice tasks (e.g., Koch et al., 2006; Leocani, Cohen, Wasserman, Ikoma, & Hallett, 2000; Tandonnet, Garry, & Summers, 2011). Moreover, a previous study used an Eriksen flanker task in which participants were instructed to respond to the direction of a central arrow while ignoring the direction of congruent or incongruent flanker arrows (Michelet, Duncan, & Cisek, 2010). The MEP amplitude was found to briefly increase in the muscle corresponding to the incorrect response when the central stimulus was accompanied with incongruent flankers (Michelet et al., 2010). These results are compatible with the notion that these visual distractors activate the incorrect response corresponding to the flankers' direction. It thus provided evidence that even an incorrect response can initially be selected and implemented.

Previous studies also showed that, in choice tasks, the amplitude of the MEP initially increased whatever the forthcoming response (e.g., Burle, Bonnet, Vidal, Possamaï, & Hasbroucq, 2002; McMillan, Ivry, & Byblow, 2006). This activity precedes the dissociation between the responding and the nonresponding hands, suggesting that both responses can be initially implemented in between-hand choice tasks (Tandonnet et al., 2011). Previous studies also raise the possibility that such early motor activation is automatic; that is, it can be triggered by the stimulus irrespective of the task requirements. Such a response-*aspecific* process received support from a previous study showing that when the hand involved in the response is known in advance and the task consists of executing this response after the occurrence of the imperative stimulus (simple reaction time task), the MEP can increase for both manual responses (Leocani et al., 2000). Such increase in MEP amplitude even for the hand not involved in the task supports the notion that sensory inputs can trigger an early activation of both responses independently of the task context.

However, such early motor activation triggered by the stimulus irrespective of the task requirements is not guaranteed. Indeed, previous studies used a task that requires executing or withholding the response as a function of the nature of the imperative stimulus (go/no-go task). These studies showed that the MEP was found to increase for the go trials but decrease for the no-go trials, suggesting an inhibitory process (Hoshiyama et al., 1996, 1997; Leocani et al., 2000; Yamanaka et al., 2002). Such lack of initial facilitation in the no-go situation raises the possibility that the early motor activation evidenced in between-hand choice tasks may critically depend on the task context. Hence, to what extent an early motor activation can be triggered by the stimulus irrespective of the task requirements has not been unambiguously determined yet.

### Early Action Implementation Specific to Potential Actions?

In the present study, we assessed whether an early motor activation specifically occurs for the potential responses involved in the task (Figure 1B). We used single-pulse TMS of the left motor cortex to probe the dynamics of the final motor pathway, as an index of action implementation relative to the right ("stimulated") hand. In different versions of reaction time tasks, we varied the potential involvement of the two hands; the same visual imperative stimuli were displayed at the same location with the same probability of occurrence. In a right go/no-go task, participants were instructed either to produce a response with the right hand when the stimulus location was on the right, or not to respond when the stimulus location was on the left, so that the stimulated hand was always the hand involved in the task. We contrasted this task with two tasks. In a between-hand choice task, the stimulated hand was possibly involved in the response, depending on the stimulus location. In a left go/no-go task, the responding hand was the left hand so that the stimulated hand was never the hand involved in the task.

Race-like models with continuous transmission assume that partial accumulation of evidence for each alternative directly leads to response implementation (Figure 1A); this predicts an initial action implementation that should be specific to the potential responses involved in the task. This "potential-responses activation" hypothesis predicts an early response-*aspecific* MEP increase only when the stimulated hand is a potential response involved in the task, that is, for right go/no-go and between-hand choice but not for left go/no-go (Figure 1B).

In contrast, race-like models with sequential transmission and diffusion-like models assume that decision making can only lead to the implementation of the selected response (Figure 1A). These models predict only a response-*specific* MEP increase when the right hand is involved in the forthcoming response (right go/no-go and between-hand choice). Hence, they predict no early response-*aspecific* MEP increase before the response-*specific* increase, whatever the potential involvement of the right hand in the task, that is, for the three tasks (Figure 1B).

The prediction of an early motor activation specific to the potential responses was also contrasted with a motor activation irrespective of the potential actions. An early motor activation "automatically" triggered by the stimulus irrespective of the task requirements would reflect a mechanism independent of the decision making. Therefore, such activation would be incompatible with the race-like models with continuous transmission. This "automatic activation" hypothesis predicts a response-*aspecific* MEP increase (with the same magnitude) whatever the potential responses, that is, even when the right hand is not a potential response (left go/no-go; Figure 1B).

We also used paired-pulse (3-ms ISI) TMS to assess whether such early motor activation involves a release of intracortical inhibition (SICI) within the motor cortex. If this is the case, the initial response-*aspecific* increase in MEP amplitude obtained with single-pulse TMS would be accompanied by an increase in the MEP ratio (i.e., the size of the conditioned MEP evoked by paired-pulse TMS relative to a control size MEP evoked by single-pulse TMS; e.g., Kujirai et al., 1993).

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## Method

### Participants

Twelve healthy participants (eight females and four males, aged 21–37 years, mean = 27) with self-reported right handedness and normal or corrected-to-normal vision volunteered for the experiment. Informed written consent was obtained according to the Declaration of Helsinki, and the study was approved by the University of Tasmania Human Research Ethics Committee.

### Behavioral Task

Participants were seated in a comfortable chair in a darkened room with supports for forearms and hands. The hands were held in a neutral position with the thumbs resting on the top of two vertical cylinders with mounted force sensors fixed on the table approximately 30 cm in front of participants. Participants faced a black panel, 80 cm distant at eye level. A horizontal row of three light-emitting diodes (LEDs) were positioned at the center of the panel; the two outer LEDs were 4 cm apart. The central LED (green) served as a fixation point, and the two outer LEDs (yellow) were the response signals.

### Trial Events and Tasks

Each trial started with illumination of the central fixation LED. After 500 ms, the fixation was switched off and the imperative stimulus consisting of one of the two outer yellow LEDs was switched on for 500 ms. This delay corresponded to the maximal reaction time allowed, after which a feedback signal was presented. If the first press exceeded four Newtons (N; i.e., corresponding to the force exerted by a weight of 400 g) was on the correct side during the time allowed for responding, the feedback was a short auditory click (1000 Hz, 50 ms in duration); otherwise, it was a longer buzz (400 Hz, 200 ms in duration). The intertrial interval was 800 ms. In the between-hand choice task, participants were instructed to execute as quickly as possible the isometric thumb press that was spatially compatible with the stimulus location, for example, left press for a stimulus on the left of fixation. In the left go/no-go task, participants were instructed to execute as quickly as possible the isometric left thumb press when the stimulus was to the left of fixation and to withhold this response when the stimulus was to the right of fixation. The same rationale was followed in the right go/no-go task, a right thumb press when the stimulus was to the right of fixation and to withhold this response when the stimulus was to the left of fixation.

### Design

Participants first performed a training session without TMS (between-hand choice task only) and then an experimental session with TMS during which they performed successively the three tasks. The task sequence was counterbalanced between participants. Each block comprised 72 trials in which each imperative stimulus (left/right) occurred 36 times in a random sequence. In the training session, EMG was recorded and blocks of trials were performed until the error rate was below 0.05 and the coefficient of variation of response latencies was below 0.15 during two consecutive blocks. In the experimental session of nine blocks (three blocks for each task), TMS was delivered at the stimulus presentation or at three other possible times individually determined from the EMG onset latencies of the responses in the last two blocks of the training session. One TMS time was at the imperative stimulus onset (t1) and the three other times were at one third (t2) and two thirds (t3) of the first decile of the EMG onset distribution and at the first decile (t4). The last three TMS times were, respectively, at 46 ms ($SD = 6$), 92 ms ($SD = 11$), and 139 ms ($SD = 17$) after stimulus onset. Within a block, 24 no-TMS trials and 48 TMS trials (i.e., 24 trials for each TMS condition: single-pulse, paired-pulse) occurred in a random sequence. Time of TMS delivery occurred in random sequence.

### Transcranial Magnetic Stimulation

TMS was delivered to the left motor cortex using a figure-of-eight coil connected to two Magstim 200 magnetic stimulators via a BiStim module (Magstim, Whitland, Dyfed, UK). The two Magstim stimulators were configured to deliver paired-pulse stimulation with an ISI of 3 ms to assess SICI (Kujirai et al., 1993). The coil was oriented tangentially to the scalp to deliver induced current in a posterior to anterior direction in the left motor cortex. The coil was initially placed at the vertex and then carefully positioned until the lowest threshold spot for provoking a small twitch in the right flexor pollicis brevis (FPB, prime mover of the thumb flexion) muscle was reached. This spot was marked on the scalp with a felt-tip pen to allow consistent coil placement during the experiment. To adjust the TMS intensity, participants were asked to maintain the position of their thumbs on the response device and relax their muscles during the delivery of TMS. The minimal TMS intensity necessary to evoke an MEP larger than 50 $\mu$V peak-to-peak in at least five of ten consecutive trials was used as resting motor threshold. The TMS intensity for single-pulse was set at the resting motor threshold. For the paired-pulse, the TMS intensity of the test stimulus was set at 120% of resting motor threshold, and the TMS intensity of the conditioning stimulus (ISI of 3 ms) was initially set at 70% of resting motor threshold and then adjusted upwards or downwards until the MEP was approximately half reduced though still present on every trial. In accordance with the recommendation of Garry and Thomson (2009), test stimulus intensity was held constant throughout the experiment. Mean resting motor threshold was 43% ($SD = 8$) of the maximal stimulator output. Mean test stimulus intensity was 52% ($SD = 9$) of the maximal stimulator output. Mean conditioning stimulus intensity was 28% ($SD = 5$) of the maximal stimulator output, corresponding to 65% ($SD = 6$) of the resting motor threshold.

### EMG and Force Recordings

Surface EMG activity was recorded from paired Ag/AgCl electrodes fixed over the FPB muscle in a belly tendon montage. The EMG signal was amplified with a gain of 1000, filtered using a 50 Hz notch filter, 20 Hz high-pass and 500 Hz low-pass (Butterworth, 12 dB/octave) filters, and digitized online at a sampling rate of 2 kHz (16-bit resolution; CED 1902, Cambridge Electronic Design, UK). The force signal was filtered using a 50 Hz notch filter and a 100 Hz low-pass (Butterworth, 12 dB/octave) filter, and digitized online at 2 kHz (16-bit resolution; CED 1902, Cambridge Electronic Design).

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### Signal Processing

The response latencies and the EMG onset latencies were measured relative to the onset of the imperative signal for the no-TMS trials. The mechanical response onset used for the reaction time corresponded to a press exceeding 4 N on one of the force sensors. The EMG onset latencies were scored by the experimenter via visual inspection (Burle et al., 2002; Van Boxtel, Geraats, Van den Berg-Lenssen, & Brunia, 1993). The trials presenting errors (i.e., side errors in choice task and false alarms or omission in go/no-go tasks; 1.4%, $SD = 1.1$) or latencies exceeding 500 ms (1.2%, $SD = 1.1$) were discarded. For EMG onset latencies, trials with EMG activity before the voluntary EMG burst were also discarded (10.7%, $SD = 6.2$). The peak-to-peak amplitude of the raw MEPs in the right FPB muscle was measured within a 50-ms analysis window from 15 ms after TMS onset for each trial whether the right hand was responding or not. Trials with EMG activity before the TMS delivery were discarded. The mean rejection percentage per TMS time was 1.8% ($SD = 3.0$), 3.5% ($SD = 6.3$), 6.4% ($SD = 9.1$), 27.0% ($SD = 12.7$), respectively. Because of large intersubject variability, raw MEP amplitudes were converted into $z$ scores before being submitted to statistical analyzes (e.g., Burle et al., 2002; van den Wildenberg et al., 2010; van Elswijk, Kleine, Overeem, & Stegeman, 2007). For each participant, his/her individual mean and standard deviation were computed for all experimental conditions, that is, task (between-hand choice and the two go/no-go tasks), TMS type (single- and paired-pulse), and time of TMS delivery (the entire time window, from stimulus onset to 139 ms following stimulus). $Z$ score was obtained for each participant and for each experimental cell by subtracting his/her individual mean and then dividing by his/her individual standard deviation. For paired-pulse TMS, raw MEP amplitudes were also expressed as ratios (MEP amplitude for paired-pulse TMS divided by MEP amplitude of single-pulse TMS) for SICI measure as this computation is commonly used to assess the size of the conditioned MEP relative to a control size (e.g., Kujirai et al., 1993).

### Statistical Analysis

The EMG onset latencies for the no-TMS trials were submitted to an analysis of variance (ANOVA) involving two within-subject factors: task type (between-hand choice, go/no-go) and stimulus location (left, right). The MEP amplitudes ($z$ scores) were submitted to a single ANOVA involving four within-subject factors: task (between-hand choice, left go/no-go, right go/no-go), TMS type (single-pulse, paired-pulse), stimulus location (left, right), and TMS time (four TMS times including the imperative stimulus onset). Both a priori comparisons and a posteriori comparisons were performed. The experiment was designed to assess a few specific a priori comparisons (orthogonal contrasts), planned before the ANOVA, that represent the direct predictions of the hypotheses: the right go/no-go and the between-hand choice tasks were analyzed together (involved) and contrasted with the left go/no-go task (not involved); and the right go/no-go task (always involved) was contrasted with the between-hand choice task (possibly involved). Scheffé's test was used for other a posteriori comparisons performed after the ANOVA. The MEP ratio (SICI) was submitted to an ANOVA involving three within-subject factors: task (between-hand choice, left go/no-go, right go/no-go), stimulus location (left, right), and TMS time (four TMS times). Greenhouse-Geisser correction was used for univariate repeated measures ANOVA tests involving more than one degree of freedom, in which case the uncorrected degrees of freedom, the corrected $p$ value, and the ε value were reported.

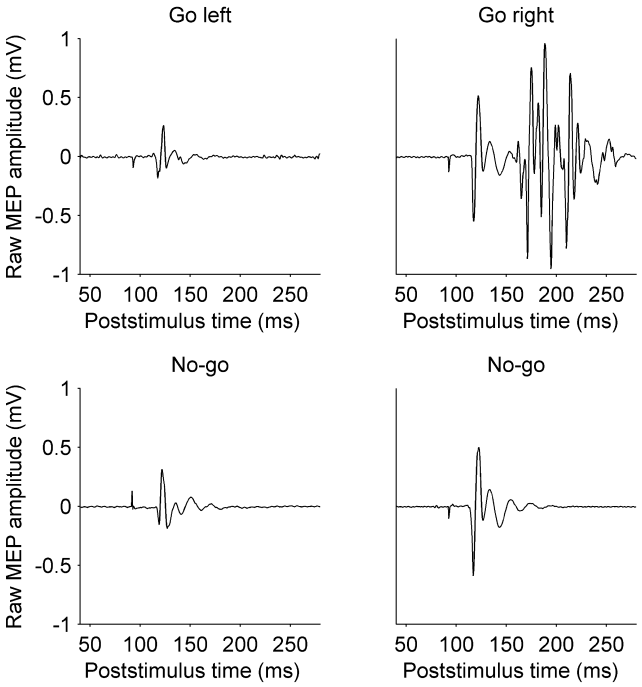


**Figure 2.** Examples of single-trial EMG traces of the right stimulated hand with raw motor evoked potential (MEP) amplitude (mV) as a function of poststimulus time (ms), for two representative tasks: left go/no-go (left column); right go/no-go (right column), and for both go (upper row) and no-go (lower row) events. For these trials, single-pulse transcranial magnetic stimulation was delivered on average at 92 ms after stimulus onset, and MEP amplitude corresponds to the mean value of each experimental condition. This figure shows the difference in MEP amplitude between the two tasks in the middle of the reaction time. Note the larger MEP amplitude when the right stimulated hand was a potential response (right go/no-go, right column) compared with left go/no-go (left column).

## Results

### Response Latency

The mean EMG onset latencies for the no-TMS trials were 177 ms ($SD = 11$). Latencies were shorter for the go/no-go tasks than for the between-hand choice task (12 ms difference, $SD = 11$; $F(1,11) = 11.8$, $p < .01$). There was no statistically significant effect of stimulus location, $F(1,11) = 3.0$, $p = .11$, and no interaction between these factors, $F(1,11) < 1$.

### MEP Amplitude

The mean amplitude of the raw MEPs for single-pulse TMS and paired-pulse TMS (3-ms ISI) was 0.81 mV ($SD = 0.78$) and 0.47 mV ($SD = 0.42$), respectively. Figure 2 presents four examples of single-trials EMG traces showing raw MEPs, for go/no-go left and go/no-go right, when single-pulse TMS pulse was delivered in the middle of the reaction time (92 ms after stimulus onset). This figure illustrates the difference in MEP amplitude between the two tasks. Figure 3 presents the mean MEP amplitudes ($z$ scores) for the three tasks and for both single- and paired-pulse TMS.

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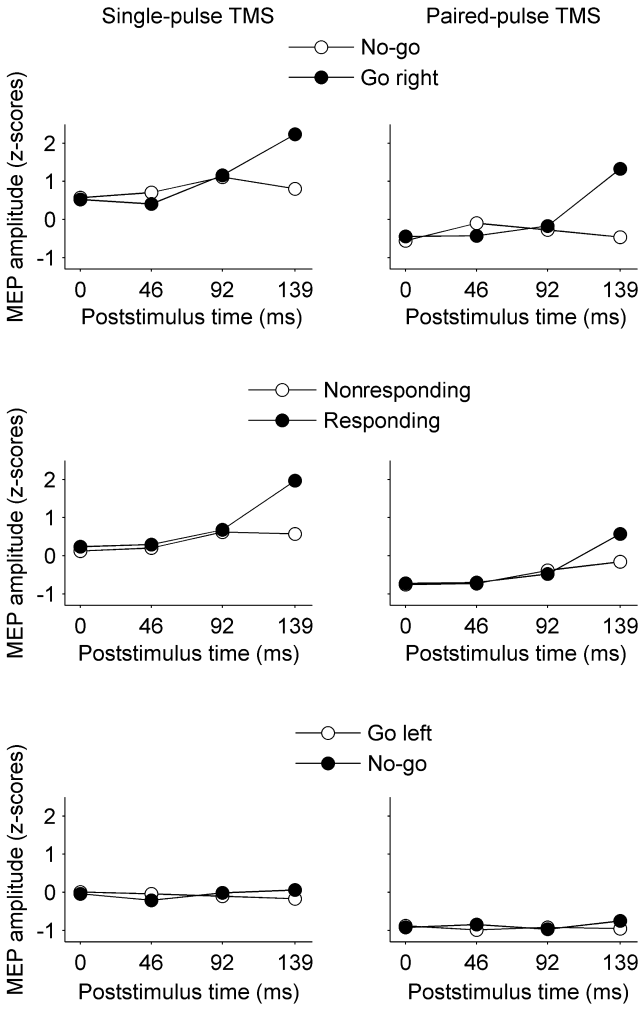


**Figure 3.** MEP amplitude (*z* scores) as a function of poststimulus time (ms) for each task: First row: right go/no-go; Second row: between-hand choice; Third row: left go/no-go. Left column: single-pulse TMS. Right column: paired-pulse TMS with 3-ms ISI. Empty dots correspond to the left stimulus location and filled dots to the right stimulus location.

Inspection of this figure revealed a similar MEP increase between 46 ms and 92 ms following stimulus presentation for both the right go/no-go and the choice tasks but no modulation for the left go/no-go task. Note that the MEP increase is early relative to the EMG onset latencies for the no-TMS trials in all tasks: right go/no-go (170 ms, $SD = 11$), choice (left: 186 ms, $SD = 14$; right: 180 ms, $SD = 18$), and left go/no-go (173 ms, $SD = 14$).

The statistical analysis is presented in two parts. The first part presents the effects on the MEP dynamics, as a function of task. The task influenced the MEP amplitude, $F(2,22) = 17.76$, $p < .01$, $\varepsilon = 0.91$. The MEP changed in amplitude during the reaction time interval, $F(3,33) = 14.75$, $p < .01$, $\varepsilon = .57$, and the MEP dynamics were different as a function of task (two-way interaction between TMS time and task; $F(6,66) = 8.71$, $p < .01$, $\varepsilon = .60$). Both hypotheses predict an increase of MEP amplitude when the stimulated hand is involved in the task (i.e., for both right go/no-go and between-hand choice tasks). The effect of time was thus assessed for both tasks together. These a priori comparisons showed no significant MEP modulation between the first two TMS times, $F(1,11) = 1.63$, $p = .23$, but a significant MEP increase between the second and the third TMS times, $F(1,11) = 7.32$, $p < .05$, and between the third and the fourth TMS times, $F(1,11) = 7.93$, $p < .05$.

The potential-responses activation hypothesis predicts that the MEP dynamics when the stimulated hand is involved in the task (right go/no-go and between-hand choice) would differ from the MEP pattern when the stimulated hand is not a potential response (left go/no-go). On the contrary, the automatic activation hypothesis predicts that the stimulus presentation would lead to a similar MEP increase when the right hand is not a potential response. The left go/no-go task was thus contrasted with both the right go/no-go and the choice tasks. These a priori comparisons revealed that the MEP dynamics for left go/no-go did not significantly differ from the MEP dynamics for right go/no-go and choice between the first two TMS times, $F(1,11) = 2.21$, $p = .17$, but did significantly differ between the second and the third TMS times, $F(1,11) = 7.56$, $p < .05$, as well as between the third and the fourth TMS times, $F(1,11) = 7.89$, $p < .05$. A posteriori comparisons further showed that there were no significant MEP modulations during the reaction time interval for the left go/no-go task ($ps > .05$).

In the potential-responses activation hypothesis, the activation can be the same when the response is part of the set of the possible responses of the task; it thus predicts a similar MEP increase for both the right go/no-go and the choice tasks. Another possibility is that the early activation can be more pronounced when the hand is always involved in the response than when the hand is one of the potential responses, hence predicting that the MEP would increase more in the right go/no-go than in the choice task. The right go/no-go task was thus contrasted with the choice task. These a priori comparisons further revealed that the MEP dynamics did not significantly differ between right go/no-go and choice during the reaction time interval, $Fs(1,11) < 1$. Thus, this first part of the analysis showed that the MEP increased when the stimulated hand is involved in the task (right go/no-go and between-hand choice tasks). In contrast, there was no significant MEP modulation during the reaction time interval when the stimulated hand is not a potential response (left go/no-go).

The second part of the statistical analysis presents, in a similar way as the first part, the effects on the response-related variations of the MEP dynamics, as a function of task. Both hypotheses predict an early response-*aspecific* MEP increase (i.e., that does not depend on the stimulus location that determines the involvement of the hand in the forthcoming response). Indeed, this MEP increase should occur before the MEP dissociation as a function of the imperative stimulus (and hence the hand involvement in the response), which was used as an index of the implementation of the selected response. The MEP amplitude was different as a function of stimulus location, $F(1,11) = 11.09$, $p < .01$, that is, for the go stimulus and the no-go stimulus (or the hand involved in the response and the hand noninvolved in the response for choice). This MEP dissociation occurred at specific times during the reaction time interval, as shown by the significant two-way interaction between stimulus location and TMS time, $F(3,33) = 15.50$, $p < .01$, $\varepsilon = .42$. The MEP dissociation may depend on the task, as suggested by the close-to-significance two-way interaction between stimulus location and task, $F(2,22) = 3.33$, $p = .067$, $\varepsilon = .82$. Moreover, the dynamics of the MEP dissociation was found to differ as a function of task, as revealed by the significant three-way interaction between stimulus location, TMS time, and task, $F(6,66) = 7.51$, $p < .01$, $\varepsilon = .60$. Both hypotheses predict that an early response-*aspecific* MEP increase and a late response-*specific* MEP increase should occur for both right go/no-go and between-

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hand choice tasks. The response-related MEP variations were thus assessed for both tasks together. These a priori comparisons showed no significant difference in MEP amplitude as a function of stimulus location for the first three TMS times ($p$s > .05) but a larger MEP amplitude for the go stimulus than for the no-go stimulus (or for the hand involved in the response than for the hand noninvolved in the response for choice) at the fourth TMS time, $F(1,11) = 17.38$, $p < .01$; see top and middle panels in Figure 3.

A priori comparisons assessed whether the response-related MEP variations were specific to the right go/no-go and the between-hand choice tasks or if they can occur for the left go/no-go task. We first present the contrast between the left go/no-go task and both the right go/no-go and the choice tasks, and then the contrast between the right go/no-go task and the choice task. The MEP pattern for left go/no-go did not significantly differ from the pattern for both right go/no-go and choice for the first three TMS times, $F$s(1,11) < 1, but these patterns differed at the fourth TMS time, $F(1,11) = 15.99$, $p < .01$. The MEP pattern for right go/no-go and choice did not significantly differ for the first three TMS times ($p$s > .05), but there was a marginally significant difference at the fourth TMS time, $F(1,11) = 4.20$, $p = .06$. A posteriori comparisons further indicate that there were no significant MEP variations as a function of the stimulus location for the left go/no-go task ($p$s > .05). Thus, this second part of the statistical analysis indicated that there was no significant response-specific MEP modulation regardless of the task until the last TMS time at which the MEP increased specifically for the hand involved in the response for both the right go/no-go and the choice tasks.

Paired-pulse TMS elicited smaller MEP amplitudes than the MEPs obtained with single-pulse TMS, $F(1,11) = 57.18$, $p < .01$, showing that the TMS parameters in the present study successfully assessed SICI. The TMS type did not interact with the other factors ($p$s > .05). Thus the MEP pattern did not significantly differ between single-pulse and paired-pulse TMS (see Figure 3).

### MEP Ratio

Figure 4 presents the mean MEP ratios (paired-pulse MEP amplitudes expressed relative to the single-pulse MEP amplitudes) for the three tasks. This figure illustrates that there was no significant modulation on this measure. The ratio for the paired-pulse TMS with 3-ms ISI showed no significant difference between the tasks, $F(2,22) = 1.40$, $p = .27$, $\varepsilon = .94$, no significant effect of TMS time, $F(3,33) < 1$, and no significant interaction between these factors, $F(6,66) < 1$. There was no significant effect of stimulus location, $F(1,11) = 2.53$, $p = .14$, with no significant two-way interaction with TMS time, $F(3,33) = 1.27$, $p = .30$, $\varepsilon = .78$, or task, $F(2,22) = 1.19$, $p = .32$, $\varepsilon = .93$, and no significant three-way interaction between stimulus location, TMS time, and task, $F(6,66) < 1$. This analysis thus suggests that the early response-*aspecific* MEP did not involve release of SICI.

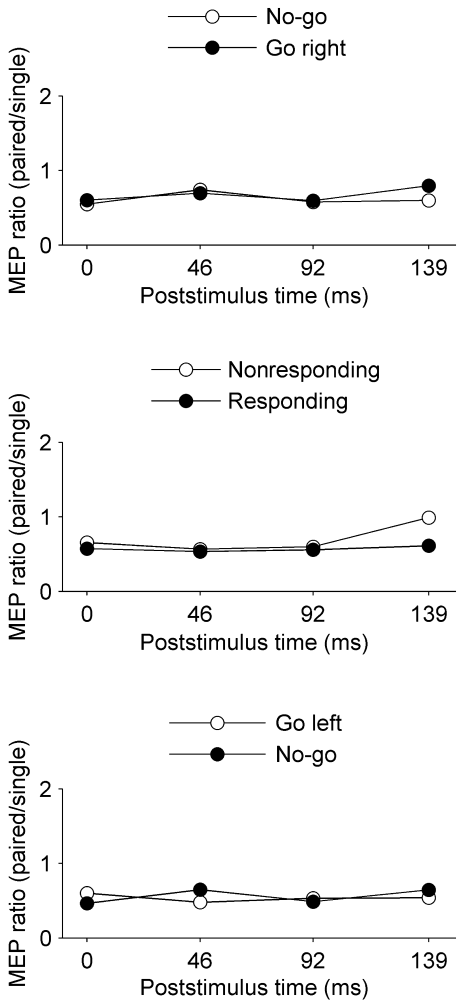


**Figure 4.** MEP ratio (paired-pulse MEPs expressed relative to single-pulse MEPs) as a function of poststimulus time (ms) for each task: First row: right go/no-go; Second row: between-hand choice; Third row: left go/no-go. Empty dots correspond to the left stimulus location and filled dots to the right stimulus location.

## Discussion

Sequential-sampling models differ by the way a decision is made and how the outcome is implemented. In the present study, to specify these mechanisms, we assessed the prediction of the race-like models with continuous transmission that an early motor activation is specific to the potential responses involved in the task (Figure 1). Single-pulse TMS of the left motor cortex was used as an index of action implementation relative to the right hand. The results showed an early response-*aspecific* MEP increase in the right hand for the right go/no-go and between-hand choice tasks but not for the left go/no-go task, that is, only for a potential response, thus supporting this prediction. We first discuss this result along with previous TMS studies, then outline the possible neural mechanisms involved in this activation, and finally describe the implications for decision-making models.

### Early Motor Activation Specific to Potential Actions

We first replicated the MEP dissociation between the responding and the nonresponding hand in the between-hand choice task (Koch et al., 2006; Leocani et al., 2000; Tandonnet et al., 2011). This pattern is compatible with an implementation of the selected alternative and a suppression of the nonselected one (Tandonnet et al., 2011). The MEP dissociation was also observed in the go/no-go task when the stimulated hand was involved in the task (right go/no-go), replicating previous studies (Hoshiyama et al., 1996, 1997; Leocani et al., 2000; Yamanaka et al., 2002). Indeed,

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these studies showed that the MEP increases in go trials and tends to decrease in no-go trials, providing evidence that the go response is activated whereas the movement to be withheld is inhibited. This pattern was also found in tasks in which a signal explicitly requires stopping a response (Coxon, Stinear, & Byblow, 2006; van den Wildenberg et al., 2010).

An early MEP increase was found prior to the MEP dissociation in the between-hand choice task, replicating previous findings (Tandonnet et al., 2011). This early response-*aspecific* activation may therefore require suppressing such an implementation of the nonselected response to ensure that only the selected response will be produced. This early activation thus provides a plausible reason why a selective suppression may occur even in choice situations that do not explicitly require stopping a response. The present study revealed that this early MEP increase occurred with a comparable dynamics in the go/no-go task when the stimulated hand was involved in the task (right go/no-go). Such early activation of the go response may require to be suppressed thereafter in the no-go trials to ensure that the movement is effectively withheld. Reciprocally, these results suggest that the context of withholding a response on half of the trials does not preclude starting to activate the go response. The similarity between the MEP modulations observed during the between-hand and the go/no-go tasks supports the notion that choice situations involve an early response-*aspecific* activation that can be selectively suppressed thereafter.

In contrast with the MEP increase in the right go/no-go task, no significant MEP modulation was found in the left go/no-go task, suggesting that the MEP increase was present only when the stimulated hand was a potential response. This pattern has not been observed previously with a similar go/no-go paradigm. In choice tasks, the imperative stimulus conveys the attribute relevant to distinguish between the two alternatives but also constitutes a task-irrelevant alerting signal that can trigger motor activation (e.g., Gottsdanker, 1975). The lack of response-*aspecific* MEP increase for the left go/no-go task provides evidence that the early MEP increase observed for the other tasks is not automatically triggered by the mere presentation of the imperative stimulus, irrespective of the alternatives, but is specific to the responses potentially involved in the task. Thus, this early motor activation likely reflects an anticipatory mechanism related to the preparation of the potential responses, and triggered by the visual stimulation. This early MEP increase supports the notion that a movement potentially involved in a choice task can be initially implemented before the response selection is complete (e.g., Cisek & Kalaska, 2005; see Cisek and Kalaska, 2010, for a review); this may occur whether the choice involves to produce or withhold a movement, or to produce a particular movement among possible ones.

In a previous TMS study, an early activation was observed in a situation in which there was no compatible correspondence between stimulus location and response location (Eriksen flanker task; Michelet et al., 2010). In the present study, the increase of the MEP in the right hand was triggered by an imperative stimulus displayed in the left hemifield (Figure 1B). Thus, the present study extends the previous finding by showing that an early response activation can be triggered by a visual stimulus when the stimulus location is spatially incompatible with the response location. In terms of dual-route architectures (e.g., Kornblum, Hasbroucq, & Osman, 1990), it suggests that the potential responses can be initially activated through a direct route independently of the spatial coding of stimulus and response attributes.

### Neural Mechanisms

An increase of the single-pulse MEP reflects a modulation in excitability of the final motor pathway, suggesting that the potential responses are implemented at the level of the final motor output. This pattern was found to be similar for single- and paired-pulse in the between-hand choice task, replicating previous findings (Tandonnet et al., 2011), and was also found in the go/no-go task. These results suggest that this early motor activation does not involve SICI. Cortical inhibition is thought to be influenced by gamma-aminobutyric acid (GABA)-ergic inhibition with modulation of the cortical silent period duration being mediated by $GABA_B$ receptors (Siebner, Dressnandt, Auer & Conrad, 1998; Werhahn, Kunesch, Noachtar, Benecke, & Classen, 1999) and SICI by $GABA_A$ receptors (Ziemann, Lönnecker, Steinhoff, & Paulus, 1996; see Ziemann, 2004, for a review). As previous studies have shown that the silent period can be shortened following stimulus presentation in between-hand choice tasks (Burle et al., 2002; Tandonnet et al., 2012), the early motor activation observed in the present go/no-go and between-hand choice tasks may involve release of intracortical inhibition mediated by circuits different than SICI and possibly those mediated by $GABA_B$ receptors. Interestingly, a response-specific suppression was evidenced in a between-hand choice task with a similar MEP pattern for single- and paired-pulse (Tandonnet et al., 2011) and can also be interpreted following the same rationale. The present results thus raise the possibility that the same neural mechanisms are involved in both the early response-*aspecific* activation and the subsequent response-*specific* suppression in choice tasks.

Neuronal activity in the premotor cortex provides a possible physiological basis of such early motor activation. Activity of neurons taking part in motor cortical structures have been recorded in the monkey in phase with visual stimuli (e.g., Rizzolatti & Luppino, 2001). These sensorimotor neurons have exemplified the involvement of the motor system in sensorimotor transformations including the decision to initiate a particular response (e.g., Rizzolatti & Craighero, 2004). Recent TMS studies have provided evidence for involvement of lateral prefrontal cortex in response selection, and dorsal premotor cortex in motor control (Duque, Labruna, Verset, Olivier, & Ivry, 2012). Thus, the dorsal premotor cortex may be responsible for the early motor activation observed in the present study. Indeed, the hypothesis that this activation is linked to changes in connectivity between the dorsal premotor cortex and the motor cortex receives support from the findings showing that such changes can be independent of intracortical circuits involved in SICI (Koch et al., 2006).

### Implications for Decision-Making Models

Sequential-sampling models differ by the way the evidence for one alternative is accumulated and by the link between decision making and action implementation. The early motor activation suggests that a potential action can initially be implemented prior to the implementation of the selected action. This activation thus supports the prediction of the race-like models assuming that partial accumulation of evidence in favor of one alternative can lead to implementation of the corresponding action (i.e., continuous transmission; Figure 1A).

In diffusion-like models, evidence in favor of one alternative is integrated against the other into a single accumulator. These models cannot therefore predict an early implementation before evidence is accumulated in favor of one alternative, making the

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present findings difficult to reconcile with these models. In contrast, in race-like models, evidence in favor of each alternative is integrated in separate accumulators, making them possibly compatible with such early response implementation. However, some race-like models, and diffusion-like models, rely on a common assumption that the selected action can be implemented only when the accumulation of evidence is complete. The present results are incompatible with this principle of sequential transmission between decision making and action implementation, unless further assumptions are added (e.g., Tandonnet et al., 2011). These findings are instead consistent with the principle of continuous transmission (e.g., Eriksen & Schultz, 1979), implying that accumulation of evidence is directly linked to action implementation, and also with the notion that accumulation of evidence directly reflects action implementation (e.g., Carpenter & Williams, 1995; Purcell et al., 2010).

## Conclusion

In the present study, the physiological index of response implementation assessed by TMS of the motor cortex provided evidence for an early motor activation. This activation was found only when the hand involved in the response execution was in the set of the potential responses of the task, suggesting that this activation reflects an anticipatory mechanism related to the preparation of the potential actions rather than an automatic mechanism triggered by the mere visual stimulation. Such early motor activation is compatible with race-like models with a continuous transmission between decision making and action implementation. In contrast, these results are difficult to reconcile with race-like models with sequential transmission and diffusion-like models, unless further assumptions are added.

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