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Top-down suppression of incompatible motor activations during response selection under conflict

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ABSTRACT

Top-down control is critical to select goal-directed actions in changeable environments, particularly when several options compete for selection. This control system is thought to involve a mechanism that suppresses activation of unwanted response representations. We tested this hypothesis, in humans, by measuring motor-evoked potentials (MEPs) elicited by transcranial magnetic stimulation (TMS) in a left finger muscle during motor preparation in an adapted Eriksen flanker task. Subjects reported, by a left or right button-press, the orientation of a left- or right-facing central arrow, flanked by two distractor arrows on each side. Central and peripheral arrows either pointed in the same (congruent trial) or in the opposite direction (incongruent trial). Top-down control was manipulated by changing the probability of congruent and incongruent trials in a given block. In the "mostly incongruent" (MI) blocks, 80% of trials were incongruent, producing a context in which subjects strongly anticipated that they would have to face conflict. In the "mostly congruent" (MC) blocks, 80% of trials were congruent and thus subjects barely anticipated conflict in that context. Thus, we assume that top-down control was stronger in the MI than in the MC condition. Accordingly, subjects displayed a lower error rate and shorter reaction times for the incongruent trials in the MI context than for similar trials in the MC context. More interestingly, we found that top-down control specifically reduced activation of the incompatible motor representation during response selection under high conflict. That is, when the central arrow specified a right hand response, left (non-selected) MEPs became smaller in the MI than in the MC condition, but only for incongruent trials, and this measure was positively correlated with performance. In contrast, MEPs elicited in the non-selected hand during congruent trials, or during all trials in which the left hand was selected, tended to increase more after the imperative signal in the MI than the MC condition. Another important observation was that, overall, MEPs were already strongly suppressed at the onset of the imperative signal and that this effect was particularly pronounced in the MI context. Hence, suppression of motor excitability seems to be a key component of conflict resolution.

Introduction

At every moment, we are faced with a large choice of actions. A key question is therefore how one action is selected in favor of another. Models of decision making postulate that the motor representations associated with the potential actions are activated in parallel and compete for selection (Cisek, 2012; Doya and Shadlen, 2012; Klein et al., 2012; Oliveira et al., 2010). Selection occurs when the activation of one action representation reaches a given threshold (Domenech and Dreher, 2010; Roitman and Shadlen, 2002). In many variants of decision-making models, the accumulation of activity for each potential response is accompanied by mutual inhibitory interactions (Brown and Heathcote, 2005; Duque et al., 2008; Praamstra and Seiss, 2005; Usher and McClelland, 2004). That is, each candidate not only accrues supporting "evidence", but also inhibits the alternative options (Coles et al., 1985; Seeley et al., 2012). Consistently, the cortical representation of non-selected responses is systematically suppressed during action selection (Burle et al., 2004; Duque et al., 2005, 2007; Meckler et al., 2010; van de Laar et al., 2012; Wijnen and Ridderinkhof, 2007).

In the context of sensorimotor decisions, perceptual evidence can sometimes lead to a strong activation of action representations that are goal-irrelevant, because irrelevant information is very salient or because these inappropriate actions are strongly appealing by nature, sometimes even more than the relevant options (Cai et al., 2012; Chen et al., 2009; Mars et al., 2009; Mattler, 2003; Michelet et al., 2010; Praamstra et al., 1998; Taylor et al., 2007). In this situation, there is a "conflict" between the goal-directed and the irrelevant actions, as evidenced by an increased time needed to provide the appropriate response and a higher error rate (Hughes and Yeung, 2011; Ridderinkhof, 2002; Takezawa and Miyatani, 2005).

When selection occurs under situations of conflict, a specific brain network, including the anterior cingulate cortex, pre-supplementary

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motor area (pre-SMA), and lateral prefrontal cortex, is engaged to help resolve competition in favor of the relevant actions (Aron, 2007; Botvinick et al., 1999; Duque et al., in press; Lenartowicz et al., 2011; Siegel et al., 2011; Young and Shapiro, 2011). The recruitment of this "top-down" control network seems to depend on the degree to which conflict is expected in advance (Cohen and Ridderinkhof, 2013; Grandjean et al., 2012; King et al., 2012). Accordingly, the ability to overcome conflict is typically larger in situations where conflict can be anticipated than when it was unlikely (Botvinick et al., 2004; Gratton et al., 1992; Ridderinkhof, 2002). Importantly, it is usually assumed that conflict resolution relies on the strengthening of inhibitory influences directed at unwanted (incongruent) response representations (Stürmer et al., 2000; Verleger et al., 2009). However, there is only indirect evidence to support this idea, both in humans (Duque et al., in press; Neubert et al., 2010; Tandonnet et al., 2011; Taylor et al., 2007) and monkeys (Cisek and Kalaska, 2005; Lecas et al., 1986). Especially relevant to the current issue is the recent finding that a TMS-induced virtual lesion to the pre-SMA, an area known to play a critical role in conflict resolution (Nachev et al., 2007; Usami et al., 2013), reduces suppression of inappropriate motor representations, especially when response selection occurs under conflict (Duque et al., in press). This indicates a link between pre-SMA functioning, conflict resolution and suppression of irrelevant representations. However, the design used in that recent study did not allow us to relate directly the strength of the motor suppression during response selection with the goal to resolve conflict. The present study aimed at addressing this point directly.

We measured motor-evoked potentials (MEPs) in a left intrinsic hand muscle while participants performed the Eriksen flanker task (Eriksen and Eriksen, 1974). Subjects were required to indicate by a left or right button-press the orientation of a briefly presented left- or right-facing central arrow, flanked by distractor arrows on each side. The central and peripheral arrows either pointed in the same (congruent trials) or in the opposite — conflicting — direction (incongruent trials). The proportion of congruent and incongruent trials was manipulated to produce two different contexts in terms of conflict expectation. In one context, most trials (80%) were incongruent ("mostly incongruent" MI context) and thus subjects anticipated that they would have to face conflict in most trials; in contrast, in the other context, a majority of trials (80%) was congruent ("mostly congruent" MC context) and thus subjects barely anticipated that they would need to overcome conflict in that condition.

Based on many previous reports, we predicted that the activation of inappropriate response representations would be larger in incongruent compared to congruent trials, especially in the MC context, due to the higher conflict in the former trial type. More importantly, we expected that this activation of inappropriate response representations would decrease in the MI context, possibly reflecting further inhibition directed at unwanted representations to resolve conflict.

Methods

Participants

A total of twenty-one subjects participated in a behavioral experiment ([$n = 9$], 6 women, mean age $= 23.2 \pm 0.72$ years old) or in a TMS experiment ([$n = 12$], 7 women, mean age $= 26.1 \pm 1.87$ years old). None of the participants had any neurological disorder or history of psychiatric illness, drug or alcohol abuse, or were on any drug treatment that could influence performance or neural activity. All the subjects were right-handed according to the condensed version of the Edinburgh Handedness Inventory (Oldfield, 1971) and were financially compensated for their participation (~35 euros per session). They were all naive to the purpose of the study. The protocol was approved by the Ethics Committee of the Université catholique de Louvain (Belgium) and all subjects gave written informed consent for their participation.

Eriksen flanker task

In both experiments, we used a modified version of the Eriksen flanker task (Eriksen and Eriksen, 1974), which was implemented by means of Matlab 6.5 (The MathWorks, Natick, Massachusetts, USA) and the Cogent 2000 toolbox (Functional Imaging Laboratory, Laboratory of Neurobiology and Institute of Cognitive Neuroscience at the Wellcome Department of Imaging Neuroscience, London, UK). Subjects were asked to respond with a left or right button-press according to the orientation of a left- or right-pointing arrow (i.e., < or >, respectively) which was briefly presented at the center of a computer screen, positioned about 60 cm in front of them. This central arrow (which we will refer to as the "target") was always flanked by a set of two distractor arrows on each side (referred to as the "flankers"); the target and the flankers either pointed in the same direction (congruent trial, "<<<<<" or ">>>>>") or in opposite directions (incongruent trial, ">><>>"or "<<><<"). Hence, subjects performed button-presses with the left or right hand in congruent and incongruent trials (4 conditions; see Fig. 1A, upper part).

As mentioned above, top-down control was manipulated by changing the probability of congruent and incongruent trials in a given block (see Fig. 1A, lower part). In the MI context, subjects had to face conflict in most trials (80% incongruent trials) whereas in the MC context, most trials did not require subjects to face conflict (80% congruent trials). Subjects were always told about the context (MI or MC) of the block they would start performing next. As a consequence, the degree to which subjects anticipated conflict, and thus the goal to resolve conflict, clearly varied in these two contexts (Ridderinkhof, 2002). Accordingly, we assume that the involvement of top-down control mechanisms recruited to overcome conflict was larger in the MI context, a condition where subjects strongly anticipated conflict, compared to the MC context, when subjects barely anticipated conflict, as previously shown (Grandjean et al., 2012; King et al., 2012).

Experimental procedure

The participants sat in front of the computer screen with both forearms in a semi-flexed position and resting on a pillow; the hands were placed palms down on a keyboard. The keyboard was turned upside-down so that subjects could press on the required buttons with the left or right index fingers (keys "F12" and "F5", respectively). After each trial, subjects were asked to place their index fingers on two small rubber pads, which were positioned on the external side of the two target buttons (see Fig. 1B). Hence, each key press required subjects to perform a brisk flexion and abduction movement of the left or right index finger. Note that a strong emphasis was put on the execution of strictly unilateral movements. The experimenter monitored this aspect of behavior by continuously looking at the electromyography (EMG) of the left and right first dorsal interosseous muscles (FDI: muscle agonist of index finger flexion and abduction) during the experiments. He provided feedback to the participant to reduce muscle activity when necessary.

Each trial started with the presentation of a warning signal, a fixation cross (+), displayed at the center of the screen for 500 ms (Fig. 1B). This signal indicated the beginning of a trial and was followed, after a 500 ms fixed delay period, by the imperative signal which consisted of one of the four possible combinations of target and flankers ("<<<<<", ">>>>>", ">><>>", "<<><<"). Subjects were asked to respond as quickly as possible following this imperative signal; the latter disappeared after 400 ms or once a response key had been pressed. Reaction times (RTs) were computed by means of a homemade hardware (PSB). In brief, the PSB is a microcontroller (μC; MSP430F249 — Texas Instrument) based system receiving VGA and keyboard events: a timer starts on specific VGA events (imperative signal) and stops on keyboard events (finger response). The μC sends the pressed key code and the timer value (128 μs resolution) to the main computer through a USB interface, providing RT measurements with very high temporal resolution. Once