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Early attentional processes distinguish selective from global motor inhibitory control: An electrical neuroimaging study

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ABSTRACT

The rapid stopping of specific parts of movements is frequently required in daily life. Yet, whether selective inhibitory control of movements is mediated by a specific neural pathway or by the combination between a global stopping of all ongoing motor activity followed by the re-initiation of task-relevant movements remains unclear. To address this question, we applied time-wise statistical analyses of the topography, global field power and electrical sources of the event-related potentials to the global vs selective inhibition stimuli presented during a Go/NoGo task. Participants (n = 18) had to respond as fast as possible with their two hands to Go stimuli and to withhold the response from the two hands (global inhibition condition, GNG) or from only one hand (selective inhibition condition, SNG) when specific NoGo stimuli were presented. Behaviorally, we replicated previous evidence for slower response times in the SNG than in the Go condition. Electrophysiologically, there were two distinct phases of event-related potentials modulations between the GNG and the SNG conditions. At 110–150 ms post-stimulus onset, there was a difference in the strength of the electric field without concomitant topographic modulation, indicating the differential engagement of statistically indistinguishable configurations of neural generators for selective and global inhibitory control. At 150–200 ms, there was topographic modulation, indicating the engagement of distinct brain networks. Source estimations localized these effects within bilateral temporo-parieto-occipital and within parieto-central networks, respectively. Our results suggest that while both types of motor inhibitory control depend on global stopping mechanisms, selective and global inhibition still differ quantitatively at early attention-related processing phases.

Introduction

Inhibitory control refers to the ability to suppress planned or ongoing cognitive or motor processes (Aron, 2007; Zheng et al., 2008). Converging evidence indicate that when the need for inhibitory control cannot be anticipated, the suppression of specific components of ongoing or prepotent movements is not achieved by selectively stopping the irrelevant parts of the movements, but rather depends on global inhibitory mechanisms with widespread effects on motor activity (e.g. Aron and Verbruggen, 2008). Current data indeed suggest a sequential model of selective inhibition wherein selective-stop signals trigger a global stopping mechanism suppressing all motor activity and subsequently, the parts of the movement that participants still have to execute are re-initiated (so-called 'Combination model', e.g. Coxon et al., 2007, 2009).

Support for this model for instance comes from Coxon et al. (2007), who instructed participants to respond to visual stimuli by pressing two buttons, each with one hand. During the task, stop signals sometimes prompted participants to withhold the response from one (selective inhibition condition) or the two hands (global inhibition condition). The results showed that the responses in the selective inhibition condition were slower than when participant responded with their two hands. The authors advanced that this 'stopping-interference effect' followed from the fact that selective inhibition was achieved by first stopping responses from the two hands with a global inhibition mechanism, and then re-initiating the movement of one hand (see also Coxon et al., 2006). Supporting that global inhibition mechanisms are not only involved when all motor responses must be suppressed but also for selective inhibitory control, Badry et al. (2009) observed a reduced motor evoked potentials of leg muscles in successful stop trials during a manual Stop Signal Task (SST; see also e.g. Cai et al., 2012 or Macdonald et al., 2012 for supporting data).

Further corroborating the Combination model of selective inhibitory control, functional neuroimaging studies revealed that selective inhibition is supported by the same neural pathway as involved in global inhibition: The so-called 'hyperdirect pathway' enables inhibiting motor activity via monosynaptic projections from prefrontal areas to the basal ganglia (Aron, 2007; Nambu et al., 2002). However, because the hyperdirect pathway inhibits large areas of the thalamus, it

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suppresses altogether task-relevant and -irrelevant movements. Thus, in selective inhibition conditions, the movements that participants had to execute to their end have to be re-initiated after the global inhibition. Consistently, functional studies showed that the patterns of brain activity associated with selective vs. global inhibition differ only at the level of the regions involved in programming and executing new movements (notably including the supplementary motor cortex), but not within the inhibitory fronto-basal network. For example, Coxon et al. (2009) used a SST task and contrasted fMRI responses to trials in which participants had to withhold the movements of either one (selective inhibition condition) or two fingers (global inhibition) in a context where most of the trials required responding with two fingers. The authors showed that while the right inferior frontal gyrus (IFG), inferior parietal and middle frontal cortices were engaged in both the selective and global inhibition conditions, the medial frontal cortex was specifically recruited for selective inhibition. Studies on response switching, in which participants had to modify their response schemes according to imperative cues, also speak in favor of the Combination model. Kenner et al. (2010) showed that switching consists of stopping the response based on the global inhibitory control network (IFG and midbrain), and then activating a new response based on the same network as in simple 'go' responses (i.e. the pre-supplementary motor area; see also Isoda and Hikosaka, 2007).

However, the precise spatio-temporal brain dynamics underlying the sequence of motor inhibition and activation processes posited in the Combination model remains unclear. To address this question, we recorded high-density EEG during a modified visual Go/NoGo task in which participants had to respond as fast as possible with their two hands to Go stimuli and to withhold the response from the two hands (global inhibition condition, GNG) or from only one hand (selective inhibition condition, SNG) when specific NoGo stimuli were presented. We contrasted electrical neuroimaging responses to the global vs selective NoGo stimuli using time-frame wise global analyses of the topography and strength of the scalp-recorded electric potential field, as well as time-frame wise statistical analyses of distributed electrical source estimations. According to the Combination model, because the same inhibitory process support selective and global inhibition, the two conditions should differ only when and where the manual response required in the SNG but not GNG condition is initiated, i.e. within the pre-supplementary motor area, at a delay corresponding to the brain-hand conduction time (ca. 150 ms) before the SNG response time. Electrophysiologically this effect should manifest as a topographic modulation because a different configurations of intracranial generators should be engaged between the two conditions.

Methods

Participants

From an initial sample size of 21 participants, eighteen right-handed young adults (9 males; aged 25 ± 3 years, mean ± SD, range: 21–29) were included in the study (see the Results section for details). Handedness was assessed using the Oldfield-Edinburgh inventory (Oldfield, 1971). Participants reported no history of neurological illness and none was under medication at the time of testing. Each participant provided written, informed consent to participate in the study. The local Ethics Committee approved all experimental procedures.

Stimuli

The stimuli were presented at the center of a computer screen at 60 cm from the participants. Stimuli were displayed in black on a gray background. A trial consisted of the presentation of a warning stimulus (empty circle) during a fixed duration of 500 ms, followed by the presentation of an imperative stimulus during 1000 ms. The imperative stimulus was either a filled circle (Go condition: 'G'; 67% of the trials), a cross in a circle (Global NoGo condition: 'GNG'; 17%), or a half right filled circle (Selective NoGo condition: 'SNG'; 17%). Then, an inter-stimulus-interval (ISI) ranging from 1500 to 2000 ms was presented (Fig. 1). Stimuli delivery and response recording were controlled with the E-prime 2.0 software.

Procedure and task

The task was a modified Go-NoGo paradigm designed to assess both selective and global inhibitory control. There were three randomly presented conditions: In the Go (G) condition, participants had to press two response buttons at the same time, one with the index of the left hand and the other with the index of the right hand. In the Selective inhibition (SNG) condition, participants had to withhold responding with the left index while responding with the right index. In the Global inhibition (GNG) condition, participants had to withhold the response from the two hands. For conditions where a button press was required (G and SNG), participants were instructed to respond as fast as possible.

Participants completed a twenty trials (12 G, 4 GNG, and 4 SNG) familiarization block before starting the main experiment. The main experiment consisted of 4 blocks of 60 trials (40 G, 10 GNG, and 10 SNG). A calibration phase of 18 trials (12 G, 3 GNG, and 3 SNG) was presented before each block. The calibration enabled inducing additional time pressure and adjusting individually the difficulty of the task (see Manuel et al., 2012; Vocat et al., 2008 for similar procedures). During the calibration phase, the maximal response time threshold (mRTT) to the Go stimuli was determined. The mRTT was calculated as 80% of the mean response time to the Go stimuli presented during the calibration phase. A feedback "Faster" was displayed when the response time was above the mRTT. At the end of each block, the percentage of response faster than the mRTT was displayed on the screen. A rest period about 60 s was proposed to the participant between each block. The experiment lasted a total of about 45 min. Two participants completed a 5th block because of difficulties in understanding the task at the beginning of the experiment.

Electrophysiological recording and data pre-processing

Continuous EEG was recorded at a sampling rate of 2048 Hz with a 64-channel Biosemi Active two amplifier system (Biosemi, Amsterdam, Netherlands). Offline analyses were performed with

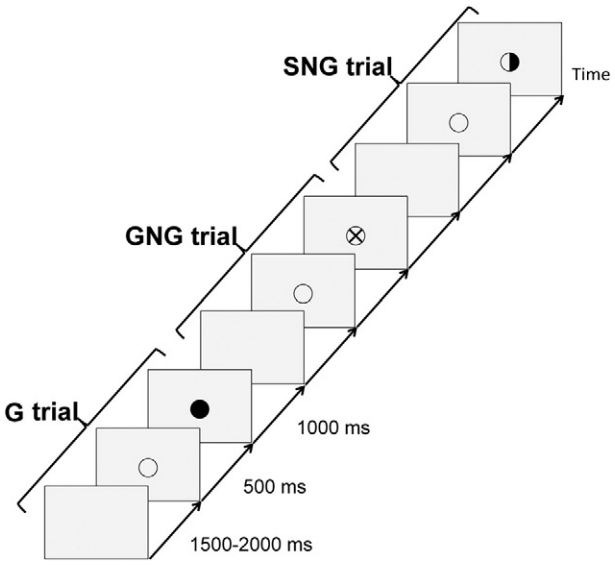

Fig. 1. Go/NoGo paradigm. Stimuli were a filled circle for the Go condition (G), a cross in a circle for the global inhibition condition (GNG) and a half right filled circle for the selective inhibition condition (SNG).