TITLE: Spatiotemporal brain signal associated with high and low levels of proactive motor response inhibition

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ABSTRACT

Proactive motor response inhibition is used to strategically restrain actions in preparation for stopping. In this study, we first examined the event related potential (ERP) elicited by low and high level of proactive response inhibition, as assessed by the stop-signal task. Corroborating previous studies, we found an increased amplitude of the contingent negative variation (CNV) in the high level of proactive inhibition. As the main goal of the present study, swLORETA was used to determine the neural generators characterising CNV differences between low and high levels of proactive inhibition. Results showed that the higher level of proactive inhibition involved numerous generators, including within the middle and medial frontal gyrus. Importantly, we observed that the lower level of proactive inhibition also involved a specific neural generator, within the frontopolar cortex. Altogether, present findings identified the specific brain sources of ERP signals involved in the later phase of motor preparation under low or high levels of proactive motor response inhibition.

Keywords: proactive motor response inhibition, EEG, ERP, swLORETA, source reconstruction modeling

INTRODUCTION

Motor response inhibition refers to the ability to stop a planned or ongoing motor action when it interferes with updated goal-driven behaviors (Aron, 2011; Aron et al., 2004, 2014; Baddeley, 1996; Logan, 1985, 1994; Verbruggen & Logan, 2009a, 2009b). This process is especially important when the individual is embedded in contexts featuring signal detection that require rapid adaptation to stop a motor response that has become inappropriate or unwanted (Aron, 2011; Verbruggen & Logan, 2009a, 2009b).

Motor response inhibition is composed of two distinct temporal dynamic modes, a *proactive* restraint in preparation for stopping and a *reactive* correction to stop ongoing action (Aron, 2011; Braver, 2012; Braver et al., 2009). Reactive inhibition is a late correction process, triggered by external signals (e.g., braking when something or somebody suddenly crosses the street) and results in the cancelling of the ongoing motor action (Aron, 2011; Braver et al., 2007, 2009; Braver, 2012). Proactive inhibition contrasts with the reactive mode in that it is used to strategically restrain actions in preparation for stopping (e.g., slowing down while cycling under bad weather conditions; Aron, 2011; Braver et al., 2007, 2009; Braver, 2012). Specifically, proactive response inhibition triggers early selection processes in which goal-relevant information is actively monitored to optimally bias attention, perception and action systems to facilitate and enhance the efficiency of motor response inhibition when needed (Aron, 2011; Duckworth et al., 2016; Fujita, 2011; Galla & Duckworth, 2015). As such, proactive inhibition might be key to the ability to refrain from behavioral tendencies in anticipating the need to stop, and seems a more ecologically valid model of daily life motor control (Aron, 2011; Chikazoe et al., 2009; Jahfari et al., 2010).

Proactive motor response inhibition can be estimated using the stop-signal task (SST), which involves the inhibition of an already started action (i.e., action cancellation of a fast go response where the go cue always precedes the stop-signal; Bari and Robbins, 2013; Eagle et al., 2008; Schachar et al., 2007; Verbruggen and Logan, 2017). Proactive inhibition can be measured during the SST as the effect of stop-signal probability on the go-signal reaction time, that is, a slowdown in responding as the probability to stop increases (Aron, 2011; Bari and Robbins, 2013; Verbuggen and Logan, 2009a, 2017; Zandbelt et al., 2011). Using a modified version of the SST, previous research from our group have shown that proactive motor response inhibition discriminates between different population, including individuals with substance or behavioral addictions (Brevers et al., 2018a), as well as among elite athletes (Brevers et al., 2018b). In line with the brain imaging literature (Aron, 2011; Chikazoe et al., 2009; Jahfari et al., 2010; Pas et al., 2017; Van Rooij et al., 2014; Vink et al., 2005, 2014; Van Belle et al., 2014; Zandbelt et al., 2010, 2011, 2013), we also showed that neural correlates of proactive motor response inhibition, as estimated by our modified SST and using functional magnetic resonance imaging (fMRI), activates an extended neural network, including the superior, middle, and inferior frontal gyrus, supplementary motor area, angular gyrus, superior parietal lobule and the striatum, in both right and left hemispheres (Brevers et al., 2017).

Nevertheless, because the time at which individuals slow down responding across different levels of proactive motor response inhibition is relatively short (between 15 and 130 milliseconds, ms; e.g., Brevers et al., 2017, 2018a,b; Zandbelt et al., 2010, 2011, 2013), the limited temporal resolution of haemodynamic imaging methods with fMRI hampers the identification of the temporal dynamics of the brain regions. EEG technique

has a more direct access to the brain's electrical activity, one of the essential mechanisms of neuronal communication. The high temporal resolution of EEG has recently allowed to characterize the brain dynamics of proactive motor inhibition (Liebrand et al. 2017). It has been shown that proactive motor inhibition was accompanied by an increased contingent negative variation potentiation (CNV), which is a marker of attentional and motor preparation (Tecce, 1972; Nagai et al., 2004).

The present study aimed to better characterize the neural bases and dynamics of proactive response inhibition by exploiting the high temporal resolution of the ERPs and recent advances in source localization. To the best of our knowledge, no ERPs studies have addressed the source localization of the ERP correlates of proactive inhibition processes. By contrast, this combination has already allowed to identify the brain areas mediating reactive inhibition as indexed by ERP components (Asadzadeh et al., 2019; Abert et al., 2013; Bodmer et al., 2018; Hong et al., 2017; Pires et al., 2014). A two-step approach was adopted. First, in order to extract the ERP signal during the SST, we employed a high-density array (false discovery rate, FDR, method for the correction of multiple comparisons across ERP signal from 128 electrodes) approach. This allowed to examine the topographic distribution of ERP while using an epoch that covers the entire length of stimulus presentation (i.e., 1250ms). Based on previous ERP findings on proactive control (Dimoska and Johnstone, 2008; Liebrand et al., 2017, 2018), and as a marker of greater response preparation (e.g., Rösler et al., 1997), we expected an increased CNV elicited by high level of proactive inhibition, as compared to low level of proactive inhibition. In the second step, we used standardized weightened Low Resolution Brain Electromagnetic Tomography (swLORETA; Palmero-Soler et al., 2007)

to identify the core network of brain regions mediating CNV under high and low levels of proactive motor response inhibition.

RESULTS

Behavioral indices of reactive Inhibition

The mean $p([\text{respond}|\text{signal}])$ was .32 (*SD* = .04) for session 1 and .38 (*SD* = .07) for session 2. SSRT scores ranged from 98.86 (minimum) to 224.49 (maximum). Repeated-measure ANOVA of SSRTs revealed no significant difference between session 1 (*M* = 159.34, SD = 33.68) and session 2 (*M* = 148.30, SD = 33.29), $F(1,45) = 2.11$, $p = .16$, $\eta^2 = .09$.

Behavioral indices of proactive inhibition

Analyses revealed that categorization RT (in milliseconds) increased in function of the level of stop-signal probability, $F(3,63) = 177.25$, $p < .001$, $\eta^2 = .89$ (see **Table 1** for descriptive statistics). Pairwise comparisons showed that were significant RT increases between each context of stop-signal probability (red > orange > yellow, green; all $p < .05$). We observed no main effect of session, $F(1,21) = 0.32$, $p = .58$, $\eta^2 = .02$, and no significant session × level interaction, $F(1,21) = 2.43$, $p = .12$, $\eta^2 = .10$.

As complementary analyses, we examined the mean percentage of misses across each level and for both sessions (see **Table 1** for descriptive statistics). Repeated measures ANOVA were used with level of stop-signal probability (green, yellow, orange, red) and sessions (1 vs. 2) as within-subject factors; and proportion of missed responses as dependent measure. Analyses revealed that mean percentage of misses increased in function of the level of stop-signal probability, $F(3,63) = 33.64$, $p < .001$, $\eta^2 = .62$. Pairwise

comparisons showed that were significant RT increases between each context of stop-signal probability (red > orange > yellow, green; all $p < .05$). We observed no main effect of session, $F(1,21) = 0.90$, $p = .35$, $\eta^2 = .04$, and no significant session × level interaction, $F(1,21) = 0.35$, $p = .78$, $\eta^2 = .02$.

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ERP analysis

Figure 2A illustrates the grand averages in the full scalp ERPs arrays for the "Low" (17 %, black lines) and the "High" (33%, red lines) stop-signal probability contexts. In the occipital scalp area, both conditions presented similar visual P100-N150 complex elicited by the apparition of the arrow on the screen (P100 of 108.6 ± 16.3ms and 4.5 ± 2.9 µV; N150 of 169.6 ± 6.9ms and -4.5 ± 3.2 µV in the low context versus P100 of 109.0 ± 17.0ms and 4.3 ± 3.1 µV; N150 of 168.9 ± 9.0ms and -4.5 ± 3.7 µV in the high context in O1 (see **Figure 2B,** where the ERPs traces of the 0% green lines and the medium 25% orange lines have also been represented). The topographic distribution of potential in the full array determined over time (in 100ms of duration steps) in both "Low" and "High" conditions revealed statistical differences ($p > 0.05$) from 600ms to the end of the epoch duration (see **Figure 2C**) involving a large CNV (illustrated in electrode C3, **Figure 2B** and **Figure 2C**). Such differences arose in central and parietal scalp areas (600 : 700ms) largely expanded over the scalp (700 : 800ms, 800 : 900ms, 900 : 1000, 1000 : 1100ms) and finally concentrated in the left hemi-scalp from parietal to precentral areas (1100 : 1200ms).

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Sources modelling

Figure 3 illustrates the nonparametric statistic maps representing the specific brain sources underlying the topographical potential distribution elicited by the apparition of the arrow in the low context condition (stop-signal probability of 17%) for the whole population and during the defined 100 ms duration period of interest calculated for each participant. The sources analysis of the Low (> High) context revealed a single significant cluster in the middle frontal gyrus of the frontal lobe with a maximum located in the Brodmann area 10 (BA10: -39.9, 49.6, 7.5).

Figure 4 illustrates the statistical maps representing the brain sources related to the High (> Low) context. Several distinct clusters were found in the frontal lobe which maxima were in the right middle frontal gyrus (BA8: 36.8, 22.5, 41.4), in the right medial frontal gyrus (BA8: 10.2, 25.4, 42.7 and BA6: 4.1, 2.5, 59.6), in the right precentral gyrus (BA6: 25.5, -15.9, 59.2). A cluster was found in the left limbic lobe with two distinct maxima in the cingulate gyrus (BA 24: -13.1, -17, 43.1 and BA31: -19.8, -28.7, 35.6). In the occipital lobe two different clusters were found in the left fusiform gyrus (BA 19: -37.9, 66.4, -6.3) and in the right superior occipital gyrus (BA 19: 33.0, -71.1, 22).

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DISCUSSION

This study aimed to examine the spatiotemporal characteristics of brain activity related to proactive motor inhibition through ERP and related reconstructed sources by exploiting the high temporal resolution of electroencephalography (EEG).

Through the use of a modified version of the stop-signal task (SST; Brevers et al., 2017, 2018a,b), we observed that participants slowed down responding as the probability that they might have to stop increased (green = 0% < yellow = 17%, < orange = 25% < red = 33%). This finding is consistent with previous studies that have examined proactive motor response inhibition with comparable experimental manipulation of stop-signal probability during the SST (Brevers et al., 2017, 2018a,b; Pas et al., 2017; Van Rooij et al., 2014; Van Belle et al., 2014; Zandbelt et al., 2010, 2011, 2013).

As the experiment stands the most powerful contrasts (assuming a linearly increasing difference as suggested by the behavioral data), we compared event-related potentials (ERPs) from the SST lower level of proactive inhibition (the yellow background context) with the highest level of proactive inhibition (the red background context). In order to extract the ERP signal, we employed a high-density array (false discovery rate, FDR, method for the correction of multiple comparisons across ERP signal from 128 electrodes) and while using an epoch that covers the entire length of stimulus presentation (i.e., 1250ms). Through this procedure, we observed stronger late CNV, in bilateral parietal to precentral areas, in the higher versus low stop-signal probability context condition. This finding is consistent with previous ERP studies (Liebrand et al., 2017, 2018), and suggest that higher attentional and motor preparation were needed to perform motor inhibition under high level inhibition probability. Indeed, CNV is a neural index of several psychomotor processes involved in transforming perceptual information into goal-directed action, including anticipatory attention and behavioral psychomotor slowing (Hillyard, 1969; Verleger et al., 2011). Accordingly,

present findings further suggest that CNV amplitude is a key biomarker of proactive control during motor response inhibition.

We then used swLORETA to identity the brain sources of CNV under high versus low level proactive motor response inhibition. One of the major advantages of modelling EEG brain sources with swLORETA is that as a distributed linear solution, it does not initially preconceive the number or the location of the calculated generators (Attal and Schwartz, 2013; Song et al., 2015, Palmero-Soler et al., 2016). The high minus low level contrast revealed significant cluster in the right/left middle frontal gyrus, the right precentral gyrus, the cingulate gyrus, the left fusiform gyrus, and the right superior occipital gyrus. These findings complement findings from previous fMRI studies on proactive motor response inhibition (Aron, 2011; Brevers et al., 2017; Chikazoe et al., 2009; Jahfari et al., 2010; Pas et al., 2017; Van Rooij et al., 2014; Vink et al., 2005, 2014; Van Belle et al., 2014; Zandbelt et al., 2010, 2011, 2013), in showing that these extended patterns of brain sources are specifically involved in the later phase of the CNV under high level of proactive motor response inhibition.

Importantly, the low minus level contrast revealed a significant cluster in the middle frontal gyrus, with maxima located in the frontopolar cortex (BA10). BA10 activation has been highlighted during a wide variety of abstract high-order cognitive functions, ranging from organization of working memory contents (Bor et al., 2003) to multitasking and theory of mind (Roca et al., 2011). BA10 activations have been shown to be triggered during self-reflection and metacognition (Fleming et al., 2012; Johnson et al., 2002; McCurdy et al., 2013), and has been proposed to allow for the conscious switching between internally and externally directed cognition (Burgess et al., 2007).

Ultimately, the BA10 is viewed as the highest point of a gradient that allows to process abstract information of high order in action-planning, that is, both more abstract (Badre and D'Esposito, 2009) and higher in an action-planning hierarchy (Koechlin et al., 2003). As such, present findings could suggest that higher-order cognitive processes subserve late phase of the CNV under low level of proactive motor response inhibition. Nevertheless, further research is needed to replicate this finding, and to shed some light on the exact nature of processes underlying the pattern of BA10 activation under low context of proactive motor response inhibition. One direction would be to undertake simultaneous EEG/fMRI recordings. This procedure is fostered by findings showing concordances between event related potential signals and hemodynamics (Chun et al., 2016). However, it still has to resolve limitations as the influence of the experimental environment inside the scanner on cognitive processes revealed by modifications of the latency ERP's components and RT responses (Chun et al., 2016).

There are several limitations to the current study. First, our modified version of the stop-signal task involved explicit manipulation of stop-signal probability (i.e., the present task is cognitively more complex than the standard stop-signal task). Hence, the complexity of the present design might have increased participants RT throughout the task. Indeed, the overall go RTs (901ms under low level of proactive inhibition, 943ms under high level of proactive inhibition) are larger than those commonly reported in the SST literature (between 500-700ms; e.g., Dimoska and Johnstone, 2007). This aspect might have influenced the optimal assessment of proactive motor response inhibition in the current stop-signal task, which is a paradigm that requires participants to respond as fast as possible (Verbruggen et al., 2019). Second, the period of interest (i.e., 100ms of

duration ending precisely at the latency of each participants individual "mean – SD" reaction time value on go trials) for brain sources modelling was not set a-priori. Hence, while such choice of period allowed to focus on the later phase of go-response motor preparation (i.e., preceding the keyboard press), it might not be purely motor free. Indeed, if one considers the readiness potential as already being related to sensory motoric processes (e.g., Vercillo et al., 2018), such components could then unfold differently across the proactive control conditions (i.e., as a factor of response speed). The use of inverse source modelling remains controversial and as every model, it has limitations (Cebolla et al., 2017) but recent human research supports the physiological plausibility of the neural generator's identification. For instance, simultaneous high-density EEG and local field potentials, recorded by electrodes implanted in the thalamus and the nucleus accumbens of patients with deep brain stimulation therapy, have recently provided direct evidence that EEG contains subcortical activity that can be reconstructed through inverse modelling (Nahum et al., 2011; Seeber et al., 2019). Hence, although brain sources modelling from EEG signals have limitations that must be taken into consideration, it may complementarily contribute with fMRI and invasive electrophysiological recordings to assess the precise dynamic brain function underlying the cognitive control of behavior. To go in depth in the information processing between the reconstructed sources it would be pertinent to approach in future studies the functional connectivity, the direction and strength of the information flow. In this context it is important to remind that the "time-varying" Granger causal connectivity approach proposed by Gao et al. (2015) would able to estimate rapid changing nonstationary processes of sources time series of ERPs.

In summary, this study used the high temporal and reasonable spatial resolution of electroencephalography source reconstruction modeling to examine the topographic and cerebral signature of the low and high levels of proactive motor response inhibition. With this procedure, we were able to identity the specific patterns of brain sources involved in the later phase of motor preparation under low or high levels of proactive motor response inhibition.

METHODS

Participants

Twenty-eight individuals (19 to 23 years of age; *mean* = 21.38, *SD* = 1.46; female = 9 male = 19) were recruited from a pool of undergraduate students at the Faculty of Motor Science of the Université Libre de Bruxelles (ULB). All participants had normal or corrected-to-normal visual acuity and were right-handed. Participants were not remunerated for their participation. All procedures performed in studies involving human participants were in accordance with the 1964 Helsinki declaration and its later amendments or comparable ethical standards. Each participant gave informed consent to the experimental procedure, which was approved by ULB Institutional Review Board.

Stop-signal Task

Participants performed two sessions of a modified stop-signal task (SST; see **Figure 1**), a paradigm adapted from previous stop-signal task designs (Brevers et al., 2017, Brevers et al., 2018a,b). Stimulus presentation and timing of all stimuli and response events were scripted using Matlab 7.14 (Mathworks Inc., Natick, MA, USA) and Psychtoolbox 3.0.12 (www.psychtoolbox.org) on a 15-inch MacBook Pro.

In this task, participants had to discriminate, as quickly as possible, between right and left arrows. Participants categorized right and left arrows by pressing the 'right arrow' or the 'left arrow' key on an AZERTY keyboard with the index and middle fingers of their right hand, respectively. Subjects were asked to stop their keyboard responses when they heard a tone (stop-signal; duration = 500ms, 44.1kHz, 16bit). During the experiment, stop-signal delay (SSD; the interval between trial onset and the presentation of the stop-signal) was continuously adjusted, separately for right and left arrows, according to a tracking procedure: if a stop response was successful, then stopping was made more difficult on the next stop-trial by increasing SSD by 25ms. The process was reversed when a stop response failed. The SSD was continually adjusted across stop-signal probability contexts; i.e., yellow, orange, red). 550ms was used as the SSD initial value based on repeated observations made during pilot testing of the task (for details, see Brevers et al., 2018b). In the current study, participants' mean SSD was 689ms for session 1 (*SD* = 78, min = 563, max = 827) and 719ms for session 2 (*SD* = 159, min = 254, max = 961).

The probability that a stop-signal would occur was manipulated across trials and was indicated by the color of the computer screen background: 0% (green), 17% (yellow), 25% (orange), and 33% (red). In order to optimize the impact of each context of stop-signal probability (i.e., green, yellow, orange, red) on proactive inhibition, we divided trials into blocks of 9, 18 or 27 trials in a same context (participants were informed that each context change occurred when a grey screen appeared). Specifically, in a pilot version of the task, we observed that reaction time difference between the different contexts of stop-signal probability was lower when the background color varied

from trial to trial. The proportion of misses on go-signal trials was also increased. One explanation is that changing the background color on each trial of the stop-signal task required the participants to reinitiate context identification on every trial, which might have lowered proactive adjustment between each context of stop-signal probability in our stop-signal task.

In the current SST, each trial started with the presentation of the probability level cue for 1100ms (**Figure 1A**). Each picture then appeared for 1250ms (**Figure 1B**), regardless of the participants' picture categorization reaction time. Each probability level change was separated by a 3350ms grey screen (**Figure 1D**). Block length was randomized with the restriction that there was no repetition of a same probability context and that blocks of 9, 18 and 27 trials occurred with equal probability. In total, 350 go-signal trials and 82 stop-signal trials were presented in a single run in pseudorandom order (total = 432 trials).

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Procedure

All participants were tested individually within a quiet room. Participants were first provided written informed consent. They were then given the following stop-signal task instructions (based on previous works by Zandbelt and colleagues, 2010, 2011):

- "Categorize left and right arrows as quickly as possible, unless you hear a "beep" sound while the picture appears on the screen."
- "Performance accuracy on the Go-signal task and Stop-signal task are equally important. It may not always be possible to suppress a response when a stop-signal occurs."

- "Stop-signals will never appear on trials with a green cue, and stop-signals could occur on trials with non-green cues. Stop-signals will be least likely in the context of a yellow cue and most likely in the context of a red cue, with orange cues signaling intermediate stop-signal probability."

Participants performed the stop-signal task while sitting in a chair, with the 15-inch laptop placed on the table in front of them. Throughout the stop-signal task, participants were instructed not to move their head and to remain still, and were asked to keep the index and middle fingers of their right hand on the 'right arrow' or the 'left arrow' key of the AZERTY keyboard. Participants first received a computerized practice session in order to familiarize them with the stop-signal task. Specifically, we needed to be sure that participants understood that it was equally important to be fast on Go-signal trials and to inhibit their motor response on Stop-signal trials. An experimenter remained alongside the participants during the training in order to ensure task comprehension. The training consisted of nine trials for each of the four stop-signal probability levels (total of 36 trials: 9 Go-signal trials under the green context, 8 Go-signal trials and 1 stop-signal trial under the yellow context, 7 Go-signal trials and 2 stop-signal trials under the orange context, 6 Go-signal trials and 3 stop-signal trials under the red context). Then, participants performed the stop-signal task a first time (session 1). After a 60-second break, participants performed the stop-signal task a second time (session 2). Importantly, the initial SSD value for session 2 was adapted from the last SSD value from session 1. This procedure was implemented to ensure continuity in task performance between sessions 1 and 2.

Behavioral data analyses

Data were analyzed using custom software in Matlab 7.14 (Mathworks Inc., Natick, MA, USA) and SPSS 24 (SPSS, Inc., Chicago, IL, USA). Reactive inhibition was indexed by the stop-signal reaction time (SSRT), a measure of the latency of the inhibition process. The SSRT was obtained through the integration method (Verbruggen & Logan, 2009b) and pooled across stop-signal probability levels > 0% (yellow, orange, red; based on Zandbelt et al., 2010, 2011). The integration method involves subtracting the mean SSD from *n*th RT (with *n* equal to the number of RTs in the RT distribution) multiplied by the overall *p* [respond|signal]). The SSRT was estimated separately for sessions 1 and 2 of the SST. We defined outliers as go trials with response times more than 1.5 times the away from the interquartile range of the 25th and 75th percentiles of the response time distribution of each stop-signal probability level. Proactive inhibition was indexed as the modulation of categorization RT by the level of stop-signal probability (green < yellow < orange < red), separately for session 1 and 2 of the SST.

Due to atypical stop-signal task participant performance, data from 4 participants were excluded as outliers (extremely high RT for stimuli categorization in the green context). In addition, due to technical issues, data from 2 participants were excluded, yielding data from 22 subjects for behavioral and EEG analyses. Statistical analysis of reactive inhibition involved repeated-measures ANOVA on SSRTs, with session (one vs. two) as a within-group factor. Statistical analysis of proactive inhibition consisted of a repeated-measures analysis of variance (ANOVA) on mean go-signal response times (mean Go-RT), with stop-signal probability context (green, yellow, orange, red), and session (one vs. two) as within-group factors. Partial eta squared (η^2) of 0.01 referred to a

small effect size, 0.06 to medium, and 0.14 to large effect size.

EEG recording parameters

EEG signals were recorded with the ANT Neuro system at a sampling frequency rate of 2048 Hz and with a resolution of 22 bits (71.5 nV per bit). An active-shield cap using 128 Ag/AgCl-sintered ring electrodes (following the 10–5 electrode system placements) and shielded co-axial cables was comfortably adjusted to each participant's head. All EEG electrodes were referred to the linked earlobes. In addition, three electrodes were used to record vertical and horizontal electro-oculograms.

EEG analysis

Off-line data treatment and statistics were performed by means of EEGLAB software (Delorme and Makeig, 2004), ASA software (ANT neuro system) and in-house MATLAB-based tools. Initially, a 512 Hz resampling, a 40 Hz low pass filter, and a 0.1 Hz high pass filter were applied. Then, any artefactual portions of the EEG data were rejected by visual inspection. Synchronous or partially synchronous artefactual activity (mostly blinks) was detected and rejected by independent component analysis (ICA) on continuous data.

As the experiment stands the most powerful contrasts (see **Figure 2B** for a display of the event related potentials, ERPs, from the green, yellow, orange, and red conditions), we analyzed the low (17% - yellow background context) and the high (33% - red background context) proactive inhibition conditions. In other words, we compared ERPs from the SST lower level of proactive inhibition (the yellow background context) with the highest level of proactive inhibition (the red background context) since they were the most interesting conditions for testing our hypotheses (i.e., increased CNV in

the high as compared to the low level of proactive inhibition). Besides, we did not compare the none (0% - green) condition with the low and high proactive inhibition conditions as it only offers a general measure of motor cautiousness (i.e., no response inhibition vs. low or high motor cautiousness), rather than an specific index of *proactive adjustment in responding* as the probability of encountering a stop event increases.

Baseline (-500ms to 0ms) corrected epochs extracted from -500ms to 1250ms of the event apparition (i.e., the left or right arrow) were calculated for the "Low" (17%) and the "High" (33%) stop-signal probability contexts. Only trials with successful go response (i.e., button press during go trials) were included. Visual inspection of the epochs allowed to reject those presenting extreme values. Epochs presenting abnormal spectra (>50 dB for 0.1–2Hz frequency band and 5–100 dB for 20–40 Hz frequency band) were also discarded in an eeglab automatic procedure. ERPs were calculated by epochs averaging for every participant. After the artifact rejection process a total of 3455 epochs for the low inhibition context (*mean* across participants = 157.04, *SD* = 14.72, min = 131, max = 194) and 2778 epochs for the high inhibition context (*mean* across participants = 126.27, *SD* = 12.54, min = 101, max = 142) remained. The significance between conditions in their topographical (128 electrodes) voltage distribution maps over time in the population was calculated by permutation analysis ($p < .05$), with the false discovery rate (FDR) method for the correction of multiple comparisons in eeglab. FDR was applied across time points when comparing the two ERP traces in single electrode and both across time points and electrodes for the topogaphical statistical plots.

Source analysis

From the distributed linear solutions available on the ASA software (ANT neuro system), we used swLORETA (standardized weightened Low Resolution Brain Electromagnetic Tomography) (Palmero-Soler et al., 2007, Pascual-Marqui, 2002) for the brain sources estimation. swLORETA allows accurate reconstruction of surface and deep current sources in simulated data even in the presence of noise and when two dipoles are simultaneously actives. This is achieved by incorporating a singular value, a decomposition-based lead field weighting that compensates for the varying sensitivity of the sensors to current sources at different depths. The method used here has been described in detail before (Cebolla et al., 2011); we computed the swLORETA solution on the individual ERP topography elicited by the apparition of the arrow picture in the low (17%) and the high (33%) stop-signal probability contexts. We settled a period of interest of 100ms of duration ending precisely at the latency of mean "Go-RT minus Standard Deviation (SD)" ms reaction time value (thus preceding the keyboard press) for each participant. In other words, each participant got their own 100ms time-window, linked to his/her individual "mean Go-RT minus SD" value. This was done separately for the 17% and the 33% stop-signal probability contexts to account for the Go-RT differences. Lastly, go trials with a key press response within the period of interest (i.e., not motor-execution free) and missed go trials (i.e., RT > 1250ms) were excluded from the analysis. Such choice of period allowed us to focus on the later stage of go-response motor preparation, and while contrasting the higher versus the lower context of proactive motor response inhibition.

The data were automatically re-referenced to the average reference as part of the LORETA inverse solution analysis and the Boundary Element Model (BEM) was formerly used for solving the forward problem. The inverse solution was restricted to the grey matter based on the probabilistic brain tissue maps available from the MNI. Voxels (10.00-mm grid size) and the electrodes arrangement were placed in registration with the Collins 27 MRI produced by the Montreal Neurological Institute. In ASA software, the corresponding Talairach coordinates are directly accessible for every voxel. The final coordinates (x,y,z, Talairach) reported in the results section correspond to maxima values of the cluster.

We used the non-parametric permutation method (Nichols and Holmes, 2002) for the statistical analysis on the sources between conditions. This method does not rely on the normality assumption and controls for the false positives that may results from performing multiple hypothesis t-tests (one for each vowel). The probability distribution for testing against the null hypothesis is calculated with the data itself. Paired t-test of swLORETA solutions were used to compare the low and the high stop-signal probability context conditions in the population. This allowed us to specify which sources were more active in each condition (*low* > *high* and *high* > *low*). The null hypothesis corresponded to the absence of difference between the compared conditions. We used the 95th percentile of the calculated permutation distribution for the maximal statistics, which defines the 0.05 level of corrected significance threshold.

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FIGURES CAPTIONS

Figure 1. An example of a succession between a neutral and a poker picture in the **(i)** green (0% stop-signal), **(ii)** yellow (17% stop-signal), **(iii)** orange (25% stop-signal) and **(iv)** red (33% stop-signal) contexts of the stop-signal task. **(A)** Each context change was separated by a 3500ms grey screen. **(B)** Each trial started with the presentation of the context cue for 1100ms. **(C)** Each picture then appeared during 1250ms, regardless of participants' categorization reaction time. **(D)** Trials were divided into runs of 9, 18 or 27 trials in a same context.

Figure 2. ERPs. **(A)** Grand average in full scalp array for the low (black traces) and high (red traces) stop-signal probability contexts. **(B)** ERPs in O1 and C3 electrodes for each stop-signal probability contexts (0% in green traces, 17% or low in black traces, 25% or medium in orange traces and 33% or high in red traces): the classical P100-N150 complex is indicated with open arrows in ERPs of O1. In ERPs traces of C3, the grey rectangle indicates the period of significant differences between low and high conditions. In the right, scalp potential topographies for both conditions illustrating the central negativity of the CNV. **(C)** Statistical differences between the low and high stop-signal probability conditions in the full array. *Notes.* The low stop-signal probability condition (i.e., the yellow background context in the SST) is colored in black for display purpose.

Figure 3. Non-parametric statistical maps of the ERP sources for the low (> high) stop-signal probability context condition calculated for the whole population taking into account individual selected periods (of 100 ms duration).

Figure 4. Non-parametric statistical maps of the ERP sources for the high (> low) stop-signal probability context condition calculated for the whole population taking into account individual selected periods (of 100 ms duration).