JNeurosci
THE JOURNAL OF NEUROSCIENCE

Research Articles: Behavioral/Cognitive

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Gerard Derosiere[1], Pierre-Alexandre Klein[1], Sylvie Nozaradan[2], Alexandre Zénon[3], André Mouraux[1] and Julie Duque[1]

[1]*Institute of Neuroscience, Université catholique de Louvain, Brussels, Belgium*
[2]*MARC Institute, Western Sydney University, Australia*
[3]*INCIA, Unité Mixte de Recherche, Centre National de la Recherche Scientifique, Bordeaux, France*

DOI: 10.1523/JNEUROSCI.0623-18.2018

Received: 7 March 2018

Revised: 28 July 2018

Accepted: 1 September 2018

Published: 10 September 2018

Author contributions: G.D., P.-A.K., and S.N. analyzed data; G.D. wrote the first draft of the paper; G.D., S.N., A.Z., A.M., and J.D. edited the paper; G.D. and J.D. wrote the paper; P.-A.K. performed research; S.N., A.Z., A.M., and J.D. designed research.

Conflict of Interest: The authors declare no competing financial interests.

This work was supported by grants from the “Fonds Spéciaux de Recherche” (FSR) of the Université Catholique de Louvain, the Belgian National Funds for Scientific Research (FRS-FNRS: MIS F.4512.14) and the “Fondation Médicale Reine Elisabeth” (FMRE). GD was a postdoctoral fellow supported by a Marie Sklodowska Curie co-fund grant (co-funded by the FNRS). PAK and SN were both PhD students supported by a FNRS grant. AZ was a Senior Research Associate supported by INNOVIRIS.

Corresponding author contact details: Gerard Derosiere, CoActions Lab, Institute of Neuroscience, Université catholique Louvain, Av. Mounier, 53 - Bte B1.53.04, 1200 Bruxelles, Belgium, Tel: + 32 (0)2 764 54 20, Email address: gerard.derosiere@uclouvain.be

Cite as: J. Neurosci ; 10.1523/JNEUROSCI.0623-18.2018

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[1] *Institute of Neuroscience, Université catholique de Louvain, Brussels, Belgium*

[2] *MARC Institute, Western Sydney University, Australia*

[3] *INCIA, Unité Mixte de Recherche, Centre National de la Recherche Scientifique, Bordeaux, France*

Corresponding author contact details:

Gerard Derosiere

CoActions Lab

Institute of Neuroscience

Université catholique Louvain

Av. Mounier, 53 - Bte B1.53.04

1200 Bruxelles, Belgium

Tel: + 32 (0)2 764 54 20

Email address: gerard.derosiere@uclouvain.be

Running title: "Conflict expectation and visuomotor cortex"

Number of pages: 50

Number of figures: 10

Number of tables: 0

Number of words: Abstract (250), Introduction (650), Discussion (1609)

Conflict of interest: The authors declare no competing financial interests.

Acknowledgements: This work was supported by grants from the "Fonds Spéciaux de Recherche" (FSR) of the Université Catholique de Louvain, the Belgian National Funds for Scientific Research (FRS-FNRS: MIS F.4512.14) and the "Fondation Médicale Reine Elisabeth" (FMRE). GD was a postdoctoral fellow supported by a Marie Sklodowska Curie co-fund grant (co-funded by the FNRS). PAK and SN were both PhD students supported by a FNRS grant. AZ was a Senior Research Associate supported by INNOVIRIS.

ABSTRACT

Many behaviors require choosing between conflicting options competing against each other in visuomotor areas. Such choices can benefit from top-down control processes engaging frontal areas in advance of conflict when it is anticipated. Yet, very little is known about how this proactive control system shapes the visuomotor competition.

Here, we used electroencephalography in human subjects (male and female) to identify the visual and motor correlates of conflict expectation in a version of the Eriksen Flanker task that required left or right responses according to the direction of a central target arrow surrounded by congruent or incongruent (conflicting) flankers. Visual conflict was either highly expected (it occurred in 80 % of trials; mostly incongruent blocks [MIBs]) or very unlikely (20% of trials; mostly congruent blocks [MCBs]). We evaluated selective attention in the visual cortex by recording target- and flanker-related steady-state visual-evoked potentials (SSVEPs) and probed action selection by measuring response-locked potentials (RLPs) in the motor cortex.

Conflict expectation enhanced accuracy in incongruent trials but this improvement occurred at the cost of speed in congruent trials. Intriguingly, this behavioral adjustment occurred while visuomotor activity was less finely tuned: target-related SSVEPs were smaller while flanker-related SSVEPs were higher in MIBs than in MCBs and incongruent trials were associated with larger RLPs in the ipsilateral (non-selected) motor cortex. Hence, our data suggest that conflict expectation recruits control processes that augment the tolerance for inappropriate visuomotor activations (rather than processes that downregulate their amplitude), allowing for overflow activity to occur without having it turn into the selection of an incorrect response.

SIGNIFICANT STATEMENT

Motor choices made in front of discordant visual information are more accurate when conflict can be anticipated, probably due to the engagement of top-down control from frontal areas. How this control system modulates activity within visual and motor areas is unknown. Here, we show that when control processes are recruited in anticipation of conflict, as evidenced by higher midfrontal theta activity, visuomotor activity is less finely tuned: visual processing of the goal-relevant location was reduced and the motor cortex displayed more inappropriate activations, compared to when conflict was unlikely. We argue that conflict expectation is associated with an expansion of the distance-to-selection threshold, improving accuracy while the need for online control of visuomotor activity is reduced.

INTRODUCTION

The physical world provides human beings and other animals with a variety of action opportunities, constantly requiring them to make choices. Recent theories posit that motor decisions emerge from a biased competition in a distributed network centered on sensorimotor structures (Derosiere et al., 2015a, 2017a, 2017b; Thura and Cisek, 2014, 2016, 2017). Following this view, a movement is initiated when sensorimotor activity favoring this action reaches a decisive selection threshold (Duque et al., 2017; Klein et al., 2012, 2016; Murphy et al., 2016).

The abundance of stimuli in the visual environment makes it often difficult to choose, especially when conflicting sources of information call for incompatible actions (Ardid and Wang, 2013). Imagine for instance a driving scenario in which a traffic light has just turned green and a child suddenly runs across the street. In such circumstances, the inappropriate action (push the accelerator pedal) and the appropriate one (push the brake pedal) are in conflict. At the behavioral level, the presence of conflict induces a cost, reflected by the reduced propensity, and prolonged time needed, to select the correct action (Chen et al., 2009; Mars et al., 2009; Taylor et al., 2007; Töllner at al., 2017). At the neural level, conflict can produce a temporary activation of inappropriate action representations in the motor system (Duque et al., 2016; Klein et al., 2014; Michelet et al., 2010; Szucs et al., 2009; Van Campen et al., 2014; Verleger et al., 2009).

In some situations, contextual cues predict the occurrence of conflict (Duque et al., 2016; Stuphorn and Schall, 2006). In the example above, a school sign will help the car driver to anticipate the appearance of children on the street. Accordingly, previous studies have shown that, by increasing conflict expectation, contextual cues help to improve accuracy when conflicting stimuli eventually occur, but tend to slow down responses in easy, non-conflicting trials (Burle et al., 2016; Duque et al., 2016; King et al., 2012; Klein et al., 2014). This

105 behavioral effect is thought to result from enhanced top-down control from frontal areas,
106 including the medial frontal area (Bartoli et al., 2017; Cohen and Ridderinkhof, 2013; Correa
107 et al., 2009; Duque et al., 2013; Spieser et al., 2015; Strack et al., 2013; Vissers et al., 2017),
108 which shows increased electroencephalography (EEG) activity in the theta range (4 to 8 Hz)
109 when conflict is expected (Van Driel et al., 2015). Yet, very little is known about the impact of
110 this control system on the competition occurring in sensorimotor areas during motor decisions.
111 Recently, a study showed that conflict expectation produces a global suppression of
112 corticospinal excitability during motor decisions (Duque et al., 2016; Klein et al., 2014).
113 Notably, this global suppression seems to occur proactively as it is already present at the onset
114 of stimulus occurrence, even before the subjects have eventually perceived the visual cue and
115 its possible conflicting nature. Further, a recent EEG study revealed a more specific suppression
116 of inappropriate motor representations (Burle et al., 2016), but the late occurrence of this effect,
117 merely around the time of movement initiation, questions its role in assisting conflict resolution.
118 Besides, very little is known about the impact of conflict expectation on sensory structures.
119 The goal of the present study was to strengthen our understanding of the sensorimotor
120 changes underlying conflict expectation by considering its impact on action selection in the
121 motor cortex and its effect on selective attention in the visual cortex. More precisely, we
122 investigated whether control processes recruited in anticipation of a visual conflict enhance the
123 selectivity of visual attention and fine-tune action selection. We used EEG to record steady-
124 state visual evoked potentials (SSVEPs) and response-locked potentials (RLPs) while
125 participants performed a modified version of the Eriksen Flanker task (Eriksen and Eriksen,
126 1974) where conflict was either highly expected or unexpected. Finally, we also considered
127 midfrontal theta activity as a marker of cognitive control during conflict expectation (Van Driel
128 et al., 2015).
129

MATERIALS AND METHODS

Participants

20 healthy human subjects participated in the study but 3 of them had to be excluded due to a hardware problem during the experiment. Hence, analyses were run on 17 subjects (9 women, 22.3 ± 2.2 years old). All participants were right-handed according to the Edinburgh Questionnaire (Oldfield, 1971) and had normal or corrected-to-normal vision. None of the participants had any neurological disorder, history of psychiatric illness, drug or alcohol abuse, or were under any drug treatment that could influence performance. Participants were financially compensated for their participation. The protocol was approved by the institutional review board of the Université catholique de Louvain, Brussels, Belgium, and required written informed consent.

Experimental design

Subjects sat on a comfortable chair in front of a 21-inches cathode ray tube computer screen, with their head supported by a chinrest at 60 cm from the monitor. The display was gamma-corrected and its refresh rate was set at 100 Hz. The left and right forearms were placed on the surface of the table with both hands on the same keyboard positioned upside-down; the left and right index fingers were located on top of the F12 and F5 keys, respectively. Participants wore a 64 Ag/AgCl electrode EEG cap placed according to the international 10/10 system during the whole experiment (Waveguard 64 cap, Cephalon A/S, Denmark). EEG signals were amplified and digitized using a sampling rate of 1000 Hz (64-channel high-speed amplifier, Advanced Neuro Technology, The Netherlands). Electrode impedances were kept below 10 kΩ. An average reference was exploited for all recordings. To monitor for artefacts from eye movements, four additional peri-ocular electrodes were placed above and below the left eye

(vertical electrooculography; EOG) and at the left and right outer canthi (horizontal EOG). Finally, an Eyelink© 1000 + eye tracker (SR Research Ltd., Kanata, Ontario, Canada; RRID: SCR_009602) was used to monitor the subjects' gaze during the experiment (sampling rate: 500 Hz). Subjects were required to maintain their gaze on the fixation point during each trial (see *Task* section, below). When deviations occurred, subjects were asked to correct their gaze position. Trials with gaze deviation were excluded from the analyses.

Task

We used a modified version of the Eriksen Flanker Task (Eriksen & Eriksen 1974; see Klein et al., 2014; Duque et al., 2016). The task was implemented by means of Matlab 6.5 (The Mathworks, Natick, Massachusetts, USA, RRID: SCR_001622) 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; RRID: SCR_015672). Subjects were required to perform a left or right index finger keypress according to the orientation of a left or right-pointing arrow (*i.e.*, < or >, respectively). This "target" was surrounded by a set of two irrelevant arrows on each side, referred to as "flankers", which either pointed in the same direction (congruent stimuli, "<<<<<" or ">>>>>") or in the opposite direction (incongruent stimuli, ">><>>" or "<<><<"; dimensions of the arrows: 18 × 18 mm; arrows were located at 2 mm from each other; whole stimulus length: 98 mm). Hence, imperative stimuli were either congruent or incongruent, and instructed either left or right index finger key-presses (four trial types; see Figure 1.A).

Each trial started with the onset of five horizontally aligned black squares (*i.e.*, 18 × 18 mm, located at 2 mm from each other; stimulus length: 98 mm) appearing 15 mm above a central point (Figure 1.B; see "SSVEP procedure" section below for an explanation regarding the slight lateralization of the squares with respect to the central point). Subjects were asked to

keep fixation on the central point during the whole trial. After 7000 ms, the squares were replaced by the imperative stimulus which consisted of one of the four possible combinations of target and flankers described above ("<<<<<", ">>>>>", ">><>>" or "<<><<"). The target always appeared at the location of the central square whereas the flankers occurred at the other square locations. In some trials (6% of total number of trials; that is, 24 trials), the imperative stimulus appeared earlier than expected (between 1000 ms and 6500 ms instead of 7000 ms). Such "catch" trials were included to make sure that the subjects were focused on the task from the beginning of each trial and ready to react as soon as the imperative stimulus appeared; these trials were not taken into account for the data analysis. Subjects were required to respond as quickly as possible following the imperative stimulus. A mask appeared once the subject had answered (or after 700 ms). The latter consisted of five aligned and overlapping double-arrows (see Figure 1.B) which remained on the screen for an interval of 1200 ms. A feedback was then presented for 1500 ms. This feedback consisted of a positive score depicted in green (following a correct response) or a negative score depicted in red (following an incorrect response). Positive scores were always inversely proportional to the RTs; the faster the response, the higher the score (score = k/RT with k = 5000). For instance, a correct response provided with a RT of 400 ms yielded a score of +12.5 points. Incorrect responses were always followed by a fixed negative score (-10). The total amount of points accumulated from the beginning of each block was also presented following each trial, just below the current trial score. Subjects knew they would receive a financial bonus depending on their final score.

Experimental blocks

All subjects came for one session of eight experimental blocks. Each block comprised the same percentage of left and right finger responses (50% left / 50% right). In contrast, the percentage of congruent and incongruent trials varied in two different block types (Figure 1.C).

In a first type of block, called "mostly congruent block" (MCB), most trials were congruent (80%) and very few were incongruent (20%). In contrast, the second block type, called "mostly incongruent block" (MIB), involved a majority of incongruent trials (80%) and few congruent ones (20%). Subjects were always told about the type of block (MCB or MIB) they would be performing next. Hence, the degree to which subjects expected conflict clearly differed between the two block types (Duque et al., 2016; Klein et al., 2014; Ridderinkhof, 2002). Conflict expectation was high in the MIBs, because subjects knew they would have to face incongruent flankers on most trials, whereas it was low in the MCBs, given the rarity of incongruent flankers in the latter blocks.

At the beginning of the session, subjects performed two blocks of forty trials in a neutral condition (same amount of congruent and incongruent trials). This allowed them to become familiar with the two trial types. Subjects then performed the eight experimental blocks (*i.e.*, four MCBs and four MIBs), each of which consisted of forty trials. The same block types were run in a row but their order was counterbalanced between subjects. Each block lasted around 7 minutes and the whole experiment duration was about 90 minutes.

SSVEP procedure

The five squares presented before the imperative signal were used to obtain SSVEPs in both contexts (MCB and MIB). The position of these squares varied on the horizontal meridian in two different block types (Figure 1.D). In half of the blocks, the five squares were slightly shifted to the left (referred to as "left-shifted" stimuli) whereas they were slightly shifted to the right in the other blocks ("right-shifted" stimuli; 10 mm of eccentricity). As a result, the central "target square" ($Target_{Sq}$) either appeared on the left or on the right side of the central fixation point (*i.e.*, on the right in right-shifted trials or on the left in left-shifted trials). This variation in the stimulus position was set to reduce any putative effect of habituation on SSVEP measures

due to the repetition of the stimulation at a given screen location (Moratti et al., 2007; Kus et al., 2013). Left- and right-shifted stimuli were grouped in separate blocks ordered in a counterbalanced way.

The squares were flickering at one of three different frequencies to induce three separate location-specific SSVEPs (flickering elicited by a contrast of luminance; Norcia et al., 2015; Vialatte et al., 2010, McTeague et al., 2015; Figure 1.D). One frequency (16.6 Hz) was selectively used to tag the $Target_{Sq}$. Another frequency (12.5 Hz) was used to tag the most central (C) "flanker square" that was located on the other side of the fixation point (Flanker-C_{Sq}; see below). A third frequency (14.2 Hz) was used for the three other flanker squares, which were more peripheral (P) with respect to the fixation point (Flanker-P_{Sq}). The flickering stopped when the arrow stimulus occurred (*i.e.*, at the end of the fixation period).

Previous studies have shown that flickering stimuli presented in one visual hemifield elicit a predominant SSVEP response in the contralateral hemisphere and an attenuated response in the ipsilateral hemisphere (*e.g.*, Kim et al., 2008, 2011). Therefore, we expected the $Target_{Sq}$ and Flanker-C_{Sq} to elicit predominant SSVEP responses in opposite hemispheres (given that they are located on opposite sides of the fixation point). For instance, in left-shifted trials, we expected the $Target_{Sq}$ and Flanker-C_{Sq} to elicit predominant SSVEP responses in the right and left hemispheres, respectively, whereas the reversed pattern was expected in right-shifted trials, as confirmed by our analyses (see Results section). Conversely, we predicted that the three Flanker-P_{Sq} would elicit comparable SSVEP responses in both hemispheres as these squares were shared out on both sides of the central fixation point. Moreover, based on previous studies, we expected the SSVEP responses to be most prominent in the signal recorded at occipito-parietal electrodes, capturing responses originating mostly in the underlying visual cortex, though parietal and frontal sources are not excluded (Di Russo et al., 2007; Gulbinaite et al., 2017; Heinrichs-Graham and Wilson, 2012; Kim et al., 2011).

The amplitude of SSVEPs is known to reflect how much visuospatial attention is allocated to the flickering stimuli, regardless of whether attention is overtly or covertly oriented towards them (Keil et al., 2006; Müller et al., 2006; Norcia et al., 2015; Shioiri et al., 2016; Vialatte et al., 2010). In the present study, we compared SSVEPs in MIBs and MCBs to investigate the influence of conflict expectation on the allocation of covert attention towards goal-relevant ($Target_{Sq}$) and goal-irrelevant (Flanker-C_{Sq} and Flanker-P_{Sq}) stimulus locations.

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Figure 1 about here

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Behavioral measurements

Data analysis

Finger responses were classified according to the responding hand (*i.e.*, left or right hand), the trial type (*i.e.*, congruent or incongruent trial) and the context (*i.e.*, MCB or MIB). For each of these conditions, we calculated the percentage of correct responses (accuracy) and their reaction time (RT). Accuracy and RT data were log-transformed for the statistical analyses in order to normalize their distribution.

Statistical analysis

Statistica software (version 7.0, Statsoft, Oklahoma, United-States, RRID: SCR_014213) was used for the analysis of the accuracy and RT data. All data were examined for normality and homogeneity of variance using Skewness, Kurtosis and Brown-Forsythe tests. RT and accuracy were analyzed separately using two three-way repeated-measure analyses of variance (ANOVA) with HAND (left, right), TRIAL (congruent, incongruent), and CONTEXT (MCB, MIB) as within-subject factors. When appropriate, Fisher's LSD post-hoc tests were used to detect paired differences. The significance level was set at $p < .05$. Results are expressed as mean ± standard error (SE).

Visuomotor activity

Data analysis

All EEG data were processed on Matlab (The Mathworks Inc. Natick, Massachusetts, USA) using Letswave 6 (Mouraux and Iannetti, 2008) and EEGLAB (RRID: SCR_007292; Delorme and Makeig, 2004). The EEG signals were filtered using a 0.01 to 70 Hz bandpass butterworth filter; they were then segmented in two subsets.

The first subset was comprised of epochs extending from +1000 to +7000 ms with respect to the onset of the 5-square stimulus. These epochs were used to extract the SSVEPs and thus served to evaluate the distribution of visual attention in space (*i.e.*, attention epochs) according to the degree of conflict expectation (larger in MIBs than in MCBs). We discarded the first 1000 ms of the flickering period to avoid contamination from the initial event-related brain potential (ERP) on the SSVEP as well as to ensure sensitivity to conditioning effects typically occurring later in the epoch (Moratti et al., 2006; Keil et al., 2013).

The second subset was comprised of epochs extending from -700 to -50 ms with respect to the onset of the key-press. These epochs were used to extract the RLPs and thus served to

characterize the motor correlates of action selection (*i.e.*, selection epochs) according to the level of conflict (larger in incongruent than in congruent trials) and the degree of conflict expectation (larger in MIBs than in MCBs). We also considered the influence of responding with the right (dominant) or left (non-dominant) hand.

For both subsets of epochs, an Independent Component Analysis (ICA) was computed to remove components corresponding to eye blinks and electrical line noise (Delorme et al., 2007); the data were then screened visually and epochs with residual artifacts were rejected.

SSVEP data

SSVEPs were obtained to evaluate visual cortical correlates of selective attention. To do so, attention epochs were first classified according to the stimulus shift (left- or right-shifted) and the context in which they were recorded (MCB, MIB). Following this classification, a total of 78 ± 4 epochs were obtained per condition. Each epoch was then sectioned in two sub-epochs of 3000 ms duration: the first sub-epoch extended from +1000 to +4000 ms and served to assess selective attention at an early stage of the fixation period ($Stage_{Early}$) while the second one, extending from +4000 to +7000 ms, served to assess attention at a later stage of fixation ($Stage_{Late}$). For each condition obtained (*i.e.*, $Stage_{Early}$/$Stage_{Late}$, left-/right-shifted, MCB/MIB), the epochs were averaged to attenuate the contribution of neural activity that was not phase-locked to the onset of the square stimulus (Derosiere et al., 2015b). A current source density (CSD) transformation was applied to the scalp voltage data to enhance the spatial specificity of the signals (Burle et al., 2015; McTeague et al., 2015; Vidal et al., 2015).

The signals were zero-padded with 2000 points in order to increase the frequency resolution of the ensuing Fast-Fourier Transform (FFT) analysis (Chabuda et al., 2018; Diez et al., 2011; Gruss et al., 2012). For each sub-epoch, the number of points was thus extended from

3000 points (*i.e.*, epochs of 3000 ms sampled at 1000 Hz; see above) to 5000 points. A discrete FFT was then applied to convert the signals in the frequency domain (Frigo and Johnson, 1998), yielding spectra from 0.1 to 500 Hz with a resolution of 0.2 Hz (Bach and Meigen, 1999). Background noise was removed by computing, for each point of the spectra, its z-score value with respect to the values measured at neighboring frequency bins (2^{th} to 5^{th} frequency bins relative to each bin; Mouraux et al., 2011; Nozaradan et al., 2011, 2012, 2017; Rossion et al., 2012).

Based on the scalp topographies and on the literature, we defined an occipito-parietal region of interest (ROI) for which SSVEP amplitudes are known to be maximal when elicited by a contrast of luminance (McTeague et al., 2015; Rossion et al., 2012). This posterior ROI (ROI_{Post}) included the O1, O2, PO3, PO4, P3, P4, P5, P6, P7 and P8 electrodes (Figure 2.A). Half of these electrodes are located over the left hemisphere (O1, PO3, P3, P5 and P7), whereas the other half are over the right hemisphere (O2, PO4, P4, P6 and P8). To assess SSVEPs emerging in the hemisphere contralateral to the $Target_{Sq}$ ($HEMI_{Contra\text{-}to\text{-}Target}$), we pooled together the data from corresponding electrodes in both hemispheres (*e.g.*, O1 and O2) collected during left- and right-shifted trials. That is, SSVEPs recorded from O2, PO4, P4, P6 and P8 (right-sided electrodes) during left-shifted trials were pooled with those obtained at O1, PO3, P3, P5 and P7 (left-sided electrodes) during right-shifted trials, respectively. The resulting "pooled" scalp locations in the $HEMI_{Contra\text{-}to\text{-}Target}$ are referred to by numbers from 1 to 5 according to the location of each pair of original electrodes, beginning with the most caudo-medial ones (ROI_{Post_1} = O1 and O2) and ending with the most rostro-lateral ones (ROI_{Post_5} = P7 and P8; see Figure 2.A). Likewise, to evaluate SSVEPs emerging in the hemisphere ipsilateral to the $Target_{Sq}$ ($HEMI_{Ipsi\text{-}to\text{-}Target}$), we pooled together the data recorded from O2, PO4, P4, P6 and P8 (right-sided electrodes) during right-shifted trials and the data recorded from O1, PO3, P3, P5 and P7 (left-sided electrodes) during left-shifted trials, respectively. The

resulting "pooled" scalp locations in the $HEMI_{Ipsi\text{-}to\text{-}Target}$ are also referred to as $ROI_{Post\_1\text{-}5}$. Note that because the $Target_{Sq}$ and Flanker-C_{Sq} were always located on opposite sides of the fixation point, the hemisphere contralateral to the Flanker-C_{Sq} was the $HEMI_{Ipsi\text{-}to\text{-}Target}$, whereas the one ipsilateral to the Flanker-C_{Sq} was the $HEMI_{Contra\text{-}to\text{-}Target}$.

Frequency spectra extracted from the ROI_{Post_1} to ROI_{Post_5} electrodes were exploited to compute linear channel maps. In Figure 2.A, the electrodes were disposed along the y-axis according to their scalp location (from ROI_{Post_1} to ROI_{Post_5}) and the spectral amplitude obtained at each frequency (x-axis) was linearly interpolated (see Langer et al., 2017, for a similar approach). In each subject, eight maps were obtained. That is, we obtained a map for each hemisphere ($HEMI_{Contra\text{-}to\text{-}Target}$, $HEMI_{Ipsi\text{-}to\text{-}Target}$), each context (MCB, MIB) and each stage of the fixation period ($Stage_{Early}$, $Stage_{Late}$).

RLP data

RLPs were obtained to evaluate motor cortical correlates of action selection. To do so, selection epochs were classified according to the responding hand (left, right), the trial type (congruent, incongruent) and the context in which they were recorded (MCB, MIB). Epochs obtained from trials where an incorrect response was provided were discarded from further analysis. Following this classification, a total of 35 ± 6 epochs were obtained per condition. For each condition, the epochs were averaged to attenuate the contribution of neural activity that was not phase-locked to the onset of the key press (Derosiere et al., 2015b) and a baseline subtraction was applied (time window for baseline correction: -700 to -500 ms). The signals were subsequently cropped at -500 ms and CSD transformation was applied to the scalp voltage data to enhance the spatial specificity of the signals (Burle et al., 2015; McTeague et al., 2015; Vidal et al., 2015).

Based on the obtained scalp topographies and on the literature, we defined a central ROI ($ROI_{Central}$) for which the RLP amplitudes are maximal close to movement execution (Cottereau et al., 2014; Clark et al., 2015). The central ROI included the C1, C2, C3, C4, C6, C7, T7 and T8 electrodes (Figure 2.B). Half of these electrodes are located over the left hemisphere (C1, C3, C7 and T7), whereas the other half are over the right hemisphere (C2, C4, C6 and T8). To assess RLPs emerging in the hemisphere contralateral to the responding hand ($HEMI_{Contra\text{-}to\text{-}Resp}$), we pooled together the data from corresponding electrodes in both hemispheres (*e.g.*, C4 and C3) collected in trials in which subjects provided left and right hand responses. That is, the RLPs recorded from C2, C4, C6 and T8 (right-sided electrodes) when subjects provided left hand responses were pooled with those obtained at C1, C3, C7 and T7 (left-sided electrodes) when they responded with the right hand, respectively. The resulting "pooled" scalp locations in the $HEMI_{Contra\text{-}to\text{-}Resp}$ are referred to by numbers from 1 to 4 according to the location of each pair of original electrodes, beginning with the most medial ones ($ROI_{Central\_1}$ = C1 and C2) and ending with the most lateral ones ($ROI_{Central\_4}$ = T7 and T8). Likewise, to evaluate the RLPs emerging in the hemisphere ipsilateral to the responding hand ($HEMI_{Ipsi\text{-}to\text{-}Resp}$), we pooled together the data recorded from C2, C4, C6 and T8 (right-sided electrodes) when subjects provided a right hand response and the data recorded from C1, C3, C7 and T7 (left-sided electrodes) when they responded with the left hand, respectively. Again, these "pooled" scalp locations in the $HEMI_{Ipsi\text{-}to\text{-}Resp}$ are referred to as $ROI_{Central\_1\text{-}4}$.

RLPs extracted from $ROI_{Central\_1}$ to $ROI_{Central\_4}$ electrodes were exploited to compute linear channel maps. In Figure 2.B, the electrodes were disposed along the y-axis according to their scalp location (from $ROI_{Central\_1}$ to $ROI_{Central\_4}$) and the amplitude of the RLP obtained at each time point (x-axis) was linearly interpolated. In each subject, sixteen maps were obtained. That is, we obtained a map for each hemisphere ($HEMI_{Contra\text{-}to\text{-}Resp}$, $HEMI_{Ipsi\text{-}to\text{-}Resp}$), for each hand

response (left, right), in the two trial types (congruent, incongruent) and in both contexts (MCB, MIB).

Statistical analysis

The SSVEP and RLP maps were analyzed using a cluster-based statistical method (Bullmore et al., 1999; Maris, 2012; Maris and Oostenveld, 2007; Poline and Mazoyer, 1993). This approach allows to run analyses on multiple data points while accounting for both the multiplicity of the statistical tests realized and the spatial dependency between the points. It was initially developed for the statistical analysis of structural magnetic resonance imaging (MRI) data (Bullmore et al., 1999; Poline and Mazoyer, 1993) and has been then extended to EEG work (Maris and Oostenveld, 2007), where it has been widely used ever since (*e.g.*, Craddock et al., 2017; Frehlich et al., 2016; Groppe et al., 2011; Melloni et al., 2015; Pernet et al., 2015).

Here, we used a cluster-based analysis of SSVEP maps to assess the effect of the factors HEMISPHERE ($HEMI_{Contra\text{-}to\text{-}Target}$, $HEMI_{Ipsi\text{-}to\text{-}Target}$), CONTEXT (MCB, MIB) and TIME (Early, Late). Besides, the cluster-based analysis of RLP maps included the factors HEMISPHERE ($HEMI_{Contra\text{-}to\text{-}Resp}$, $HEMI_{Ipsi\text{-}to\text{-}Resp}$), HAND (left, right), TRIAL (congruent, incongruent) and CONTEXT (MCB, MIB). Note that the factor TRIAL was not included in the analysis of the SSVEPs as the imperative arrows (determining the trial type) only appeared after the flickering period.

Concretely, in a first step, a point-by-point ANOVA is performed using the factors mentioned above, hence yielding F- and p-values for each data point. Points with an F-value exceeding an alpha level of $p = .05$ are selected. Among the selected points, those that are located next to each other on the map are grouped together in clusters. For each cluster so

obtained, cluster-level F-values are subsequently computed by adding up the F-value associated with each individual data point comprised in the cluster.

Then, in a second step, Monte-Carlo permutation tests are performed. For each subject, maps are randomly permuted, resulting in a so-called "random partition" (separate analyses on SSVEP and RLP maps). This step can be considered as equivalent to randomly switching the labels of the maps, independently for each subject. Based on the random partition, a point-by-point ANOVA is performed in the exact same manner as during step 1 and cluster-level F-values are computed. The random partitioning and the subsequent calculation of the cluster-level F-values are re-iterated 1000 times. A histogram of the F-values is then constructed. For each factor and interaction tested, the proportion of random partitions that results in larger F-values than the one observed in the first step of the analysis is finally calculated. This proportion represents the Monte-Carlo significance probability, also called p-value. If, for a given effect and a given point, less than 5 % of the random partitions results in a larger F-value than the one observed in the first step of the analysis, then it is considered as significant for that cluster at $p < .05$.

For each factor and interaction, the analysis outputs a map highlighting the cluster(s) that survived to the thresholding at the Monte-Carlo significance probability. Based on these maps, the onset and offset of the cluster(s) can be estimated. Note however that the onset and offset of where each cluster exceeds the threshold depends on several factors including the frequency / temporal resolution of the SSVEP / RLP maps. Hence, when referring to the cluster edges in the followings, one should be aware that they could have slightly varied if different parameters had been exploited during data processing.

Importantly, combining a cluster-based approach with Monte-Carlo permutations allowed us to identify the data points, within the SSVEP and RLP maps, showing a significant effect of the factors mentioned above in a data-driven way (*i.e.*, by testing all the points of the maps).

Such a data-driven approach prevented us from arbitrarily selecting a number of frequency or temporal bins from the continuous signals of the SSVEP and RLP maps, respectively, and from a priori averaging the signals across the ROI_{Post} or $ROI_{Central}$ electrodes, as both procedures could have impacted the statistical results (Cohen and Gulbinaite, 2017; Pernet et al., 2015; Shen et al., 2017).

When a significant effect involved more than two conditions, post-hoc tests were required to test which pairwise difference(s) drove the statistical difference detected. For each condition, the values of every data point composing the detected cluster were averaged into a single value; Fisher LSD post-hoc tests were used to detect paired differences on the averaged values. The significance level was set at $p < .05$. Results are expressed as mean ± standard error (SE).

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Figure 2 about here

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Midfrontal theta activity

Data analysis

Conflict expectation has been shown to increase midfrontal theta activity (*i.e.*, [4 - 8 Hz]; Van Driel et al., 2015), a well-known substrate of cognitive control (*e.g.*, Gulbinnaite et al., 2014; Lin et al., 2018; Vissers et al., 2018; Wang et al., 2017). While the primary aim of the present study was to investigate the impact of conflict expectation on visuomotor activity, we also tested whether the effect reported on midfrontal theta activity could be replicated based on our dataset. To do so, we exploited the same time-frequency (TF) analysis as in Van Driel et al.

(2015) and applied it on the EEG signals obtained during the fixation period (same epoch as for the SSVEPs).

First, attention epochs (*i.e.*, as defined in the SSVEP section) were classified according to the context in which they were recorded (MCB, MIB). Second, EEG signals were decomposed into their TF representations for both contexts, every electrode and each subject. TF maps were obtained by multiplying them with a series of Morlet wavelets with frequencies ranging from 4 to 9 Hz in 20 linearly scaled steps. The wavelets were generated by multiplying perfect sine waves (sine wave = $e^{i2\pi ft}$, where i is the complex operator, f is the frequency, and t is time) with a Gaussian (Gaussian = $e^{-t2/2\sigma2}$, where σ is the width of the Gaussian). The width of the Gaussian was set to four cycles [$\sigma = 4/(2\pi f)$], in order to trade-off temporal and frequency resolution. The FFT was applied to both the EEG signals and the Morlet wavelets, and these were then multiplied in the frequency domain, after which the inverse FFT was applied. From the resulting complex signal Z_t, an estimate of frequency-specific amplitude at each time point was defined as [real$(Z_t)^2$ + imag$(Z_t)^2$]. Third, trials were averaged together, resulting in one TF map per condition, per electrode and per subject. Finally, in order to make the data comparable across all frequencies and subjects, difference maps were computed by subtracting the spectral amplitude (SpectAmp) obtained at each TF point in the MCB condition from the corresponding values in the MIB condition (Castro et al., 2018). Hence, this analysis yielded one TF map per electrode and per subject, on which the difference in spectral amplitude between MIBs and MCBs was represented (ΔSpectAmp). ΔSpectAmp values higher than 0 denoted a higher spectral power in MIBs compared to MCBs.

Statistical analysis

The statistical analysis was realized on the TF map obtained at the Fz electrode, for which the effect of conflict expectation on theta activity is the strongest (Van Driel et al., 2015, see

493 also Herz et al., 2017). A cluster-based analysis was performed in the exact same way as
494 described above on this TF map, except that we used a two-way Student's t-test against 0 (*i.e.*,
495 instead of an ANOVA). The aim of this analysis was to detect the cluster(s) of data points on
496 the TF map for which ΔSpectAmp values were higher than 0 at the Monte-Carlo significance
497 probability of .05.

498

499 **RESULTS**

500 **Behavior**

501 *Accuracy*

502 The ANOVA performed on the accuracy data revealed a tendency towards a significant
503 effect of the factor HAND ($F_{1,16} = 4.13$, $p = .059$). In fact, the percentage of correct responses
504 tended to be lower when the imperative stimulus required a left than a right hand movement
505 (84.78 ± 2.48 and 91.47 ± 1.09 % of correct responses, respectively; both trial types and
506 contexts pooled together; log-transformed data are represented on Figure 3.A). Hence, subjects
507 tended to be less accurate when they had to respond with the non-dominant hand compared to
508 when they had to answer with the dominant one. In other words, they were more prone to
509 respond with the dominant hand even when the target arrow instructed them to make the
510 opposite choice.

511 The ANOVA also revealed a significant main effect of the factor TRIAL on the accuracy
512 data ($F_{1,16} = 16.56$, $p = .0008$). The percentage of correct responses was lower in incongruent
513 (79.59 ± 2.72 %) than in congruent trials (96.67 ± 0.97 %, both hands and contexts pooled
514 together; Figure 3.B). Hence, as expected, subjects made more errors when the flankers pointed
515 to the incorrect response compared to when they pointed to the correct one.

Importantly, the TRIAL effect reported above depended on the CONTEXT within which the responses were provided (MCB or MIB), as revealed by a significant TRIAL*CONTEXT interaction ($F_{1,16}$ = 22.82, p = .0002). In fact, the difference in accuracy between congruent and incongruent trials was attenuated in the MIBs compared to the MCBs. That is, subjects made much less errors in the presence of incongruent flankers when the latter had been anticipated (in MIBs, 85.06 ± 2.68 % of correct responses) compared to when incongruent flankers were unlikely (MCBs, 74.11 ± 3.31 %, p < .00001; both hands pooled together; Figure 3.C). Hence, control processes associated with conflict expectation helped subjects to reduce the negative impact of incongruent information on their decision accuracy, as previously shown (Burle et al., 2016; Duque et al., 2016; King et al., 2012; Klein et al., 2014). Notably, congruent trials were associated with a comparable accuracy in MIBs (95.65 ± 1.74 %) and MCBs (97.68 ± 0.63 %; p = .426).

Reaction time

The ANOVA revealed a significant main effect of the factor HAND on the RT data ($F_{1,16}$ = 11.45, p = .004), with longer response times for left (500 ± 12 ms) than right hand movements (482 ± 11 ms; both trial types and contexts pooled together; log-transformed in Figure 3.D). Hence, it took more time for the subjects to respond when the target indicated a non-dominant hand response compared to when a movement with the dominant hand was required. These findings are in agreement with the accuracy data indicating a preference for responding with the dominant hand.

As expected, the ANOVA also showed a significant main effect of the factor TRIAL ($F_{1,16}$ = 91.06, p < .00001); RTs were longer in incongruent (548 ± 17 ms) than in congruent trials (435 ± 7 ms, both hand and contexts pooled together; Figure 3.E). Interestingly, this TRIAL effect also depended on the CONTEXT within which the responses were provided, as revealed

by a significant TRIAL*CONTEXT interaction on the RT data ($F_{1,16}$ = 11.52, p = .003). As depicted in Figure 3.F, the RT difference between congruent and incongruent trials was attenuated in MIBs compared to MCBs. Interestingly, this effect was not due to a fastening of response times on incongruent trials; the latter trials were associated with comparable RTs in MIBs (544 ± 19 ms) and MCBs (551 ± 18 ms; p =.209). In contrast, RTs on congruent trials varied between the two block types; they were significantly longer in MIBs (445 ± 8 ms) compared to MCBs (424 ± 8 ms; p = .003). Hence, control processes associated with conflict expectation did not allow subjects to respond faster. On the contrary, they tended to slow down RTs following congruent signals.

Notably, the scores provided at the end of each trial tended to be higher in MIBs (average score: 8.50 ± 0.46 a.u) than in MCBs (average score: 7.79 ± 0.40 a.u.), consistent with the higher accuracy in the former block types. However, this effect was not significant. ; $t_{1,16}$ = -1.839; p = .084). This negative finding may be explained by the fact that the scores not only depended on the accuracy (which showed a main effect of BLOCK; $F_{1,16}$ = 7.33, p = .01) but also relied on the reaction time (which was comparable in both BLOCK types; $F_{1,16}$ = 1.15, p = .30). Hence, overall, the feedback was roughly comparable in MCBs and in MIBs.

In conclusion, the behavioral data indicate that conflict expectation is associated with the recruitment of control processes that enhance the ability to solve conflicting visuomotor choices. However, this amelioration occurs at the cost of speed: subjects become more accurate on incongruent trials but respond more slowly to easy, congruent signals.

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Figure 3 about here

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Midfrontal theta activity

The cluster-based statistical analysis revealed that ΔSpectAmp was significantly different from 0 for a cluster of data points (*i.e.*, cluster thresholded at the Monte-Carlo significance probability of .05; Figure 4.A). The cluster extended from +4700 to +5400 ms and from 6 to 8 Hz, hence largely overlapping with the theta range (*i.e.,* [4 – 8 Hz]). Visual inspection of the grand-average TF map obtained for the Fz electrode (Figure 4.B) indicates that the ΔSpectAmp was positive in this TF window, revealing a higher spectral amplitude in MIBs than in MCBs. Further, visual inspection of the topography (Figure 4.C) suggests that this effect is restricted to the Fz electrode: ΔSpectAmp was higher at Fz than at any other midline electrodes. To provide statistical evidence for this observation, the values of each data point composing the cluster were averaged into a single value for the Fz, the Fpz (anterior to Fz), and the Cz (posterior to Fz) electrodes. An ANOVA performed on these average ΔSpectAmp values revealed a significant effect of the factor ELECTRODE ($F_{2,30}$ = 5.58, p = .008); Fisher LSD post-hoc tests showed that ΔSpectAmp was indeed significantly higher at Fz (140.88 ± 25.63 $\mu V/m^2$) than at both Fpz (-36.56 ± 58.41 $\mu V/m^2$; p = .006) and Cz (-33.08 ± 36.47 $\mu V/m^2$; p = .007), with no significant difference between Fpz and Cz (p = .954; Figure 4.D). Hence, consistent with previous findings in the literature (Van Driel et al., 2015), conflict expectation increased midfrontal theta activity in the present study, corroborating the idea that it represents an important marker of cognitive control (Gulbinnaite et al., 2014; Herz et al., 2017; Lin et al., 2018; Vissers et al., 2018; Wang et al., 2017).

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Figure 4 about here

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Visuomotor activity

SSVEP data

The cluster-based statistical analysis revealed a significant main effect of the factor HEMISPHERE on two clusters of data points (cluster thresholded at the significance probability of .05; Figure 5.A). A first cluster was centered on the $Target_{Sq}$ frequency ([16.4 Hz - 16.8 Hz]) and spread over the five $ROI_{Post\_1\text{-}5}$ locations (Figure 5.C). As expected, the SSVEP amplitude was higher in this frequency range for the $HEMI_{Contra\text{-}to\text{-}Target}$ than for the $HEMI_{Ipsi\text{-}to\text{-}Target}$ ($p < .0001$). A second cluster was centered on the Flanker-C_{Sq} frequency ([12.3 Hz - 12.7 Hz]) and extended from ROI_{Post_2} to ROI_{Post_5}. Here, the SSVEP amplitude was lower for the $HEMI_{Contra\text{-}to\text{-}Target}$ than for the $HEMI_{Ipsi\text{-}to\text{-}Target}$ ($p = .0009$; Figure 5.B). This was expected given that the two hemispheres are, respectively, ipsilateral and contralateral to the Flanker-C_{Sq} (see Method section). Hence, both the $Target_{Sq}$ and the Flanker-C_{Sq} elicited predominant SSVEP responses in the contralateral hemisphere. Such an effect of HEMISPHERE was not observed for the Flanker-P_{Sq} frequency (*i.e.*, at 14.2 Hz), consistent with the fact that these squares were located on both sides of the central fixation point.

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Figure 5 about here

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612 Interestingly, the cluster-based analysis also showed a significant main effect of the factor
613 CONTEXT (cluster thresholded at the significance probability of .05; Figure 6.A). The cluster
614 was centered on the Flanker-P_{Sq} frequency ([14.0 Hz - 14.4 Hz]) and expanded from ROI_{Post_1}
615 to ROI_{Post_3} (Figure 6.B). In this cluster, SSVEP amplitude was lower in MCBs than in MIBs
616 ($p = .013$), suggesting a surprisingly higher attention toward goal-irrelevant locations when
617 conflict was expected compared to when it was unlikely.

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619 **********

620 *Figure 6 about here*

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623 Finally, the cluster-based analysis revealed a significant effect of the factor TIME on a
624 cluster centered on the $Target_{Sq}$ frequency ([16.4 Hz - 16.8 Hz]) and expanding from ROI_{Post_2}
625 to ROI_{Post_5} (cluster thresholded at the significance probability of .05); here, the SSVEP
626 amplitude appeared to be higher at $Stage_{Late}$ than at $Stage_{Early}$ ($p < .0001$). However, this effect
627 of TIME depended on both the HEMISPHERE and the CONTEXT considered; there was a
628 significant HEMISPHERE*CONTEXT*TIME interaction on a cluster of data points centered
629 over the $Target_{Sq}$ frequency ([16.4 Hz - 16.8 Hz]) and expanding from ROI_{Post_4} to ROI_{Post_5}
630 (cluster thresholded at .05; Figure 7.A), thus overlapping largely with the data points showing
631 the main effect of TIME. Interestingly, Fisher LSD post-hoc tests revealed that although
632 SSVEPs were comparable in both contexts at $Stage_{Early}$, whether considering the $HEMI_{Contra\text{-}to\text{-}}$
633 $_{Target}$ ($p = .503$) or the $HEMI_{Ipsi\text{-}to\text{-}Target}$ ($p = .157$), they became different in both block types at
634 $Stage_{Late}$. In fact, the SSVEP amplitude in the $HEMI_{Contra\text{-}to\text{-}Target}$ was surprisingly lower in MIBs
635 than in MCBs at this later stage ($p = .002$). Consistently, the SSVEP amplitude increased in the

636 $HEMI_{Contra\text{-}to\text{-}Target}$ from $Stage_{Early}$ to $Stage_{Late}$ in MCBs ($p = .0008$) while it remained stable in
637 MIBs ($p = .879$). Such an increase from $Stage_{Early}$ to $Stage_{Late}$ did not occur in the $HEMI_{Ipsi\text{-}to\text{-}}$
638 $_{Target}$, neither in MCBs ($p = .669$) nor in MIBs ($p = .072$), hence leading to comparable SSVEP
639 amplitudes in both contexts in the $HEMI_{Ipsi\text{-}to\text{-}Target}$ at $Stage_{Late}$ ($p = .988$).

640 Hence, the SSVEP data indicate that control processes recruited in anticipation of conflict
641 do not narrow or strengthen visual attention towards the goal-relevant stimulus location. On the
642 contrary, $Targets_{Sq}$ SSVEP responses were smaller in MIBs compared to MCBs in the late stage
643 of the fixation period. Besides, Flanker-P_{Sq} SSVEP responses were globally higher in MIBs
644 than in MCBs. These results indicate a reduction of the focus of selective attention in MIBs.
645 Therefore, the higher accuracy of subjects in incongruent trials of MIBs cannot be accounted
646 for by an enhanced selectivity of visual attention.

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648 **********

649 *Figure 7 about here*

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652 *RLP data*

653 Our cluster-based analysis revealed a significant main effect of the factor HEMISPHERE
654 on two clusters of data points (cluster thresholded at $p < .05$; Figure 8.A). A first cluster
655 extended from -350 to -200 ms with respect to movement onset and concerned the $ROI_{Central\_1\text{-}}$
656 $_{2}$ locations. Interestingly, in this time window, the RLP amplitude was higher (*i.e.*, more
657 negative) in the $HEMI_{Ipsi\text{-}to\text{-}Resp}$ than in the $HEMI_{Contra\text{-}to\text{-}Resp}$ ($p < .0001$; Figure 8.B). Then, a
658 later cluster expanded from -150 to -50 ms and concerned $ROI_{Central\_1\text{-}3}$: in this time window,
659 the RLP amplitude was higher in the $HEMI_{Contra\text{-}to\text{-}Resp}$ than in the $HEMI_{Ipsi\text{-}to\text{-}Resp}$ ($p < .0001$,

660 respectively; Figure 8.B). Hence, on average, subjects initially showed a higher activity in the
661 motor cortex ipsilateral to the responding hand, compared to the contralateral one. The pattern
662 then reversed, with activity becoming stronger in the contralateral motor cortex as movement
663 execution drew nearer.

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667 *Figure 8 about here*

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671 Notably, the HEMISPHERE effect reported above on the first cluster (*i.e.*, from -350 to -
672 200 ms before movement onset) depended on the type of TRIAL the subjects encountered and
673 on the HAND they selected; there was a significant HEMISPHERE*HAND*TRIAL
674 interaction on a cluster of data points centered over the $ROI_{Central\_2}$ location and extending from
675 -320 to -150 ms, thus overlapping largely with the data points showing the HEMISPHERE
676 effect (cluster thresholded at $p < .05$; Figure 9.A).

677 In congruent trials, we observed a preponderant ipsilateral activity whether the subjects
678 responded with the left (*i.e.*, significant difference between $HEMI_{Ipsi\text{-}to\text{-}Resp}$ and $HEMI_{Contra\text{-}to\text{-}}$
679 $_{Resp}$: $p = .012$) or the right hand ($p = .051$; Figure 9.B, C and D). Hence, action selection in the
680 flanker task involved an initial predominant increase in the activity of the ipsilateral motor
681 cortex, even in the absence of conflict.

Interestingly, in incongruent trials, this pattern of activity was observed for left (significant difference between $HEMI_{Ipsi\text{-}to\text{-}Resp}$ and $HEMI_{Contra\text{-}to\text{-}Resp}$: $p < .0001$) but not for right hand responses ($p = .36$; Figure 9.B, C and D). Accordingly, left hand responses were associated with a larger activity in the $HEMI_{Ipsi\text{-}to\text{-}Resp}$ than right hand trials ($p = .0004$). Hence, in the presence of conflict, ipsilateral activity was more pronounced in the dominant (left) motor cortex (preceding left hand responses) than in the non-dominant (right) one (preceding right hand responses). Notably, a similar effect was observed for the $HEMI_{Contra\text{-}to\text{-}Resp}$: contralateral activity was larger in the dominant (left) motor cortex (preceding right hand responses) than in the non-dominant (right) one (preceding left hand responses; $p = .019$). Altogether, these results indicate that incongruent trials are associated with a stronger activation of the dominant motor cortex compared to the non-dominant one, regardless of whether the response has to be provided with the right (dominant) or the left (non-dominant) hand.

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Figure 9 about here

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Finally, our analysis also revealed a significant HEMISPHERE*TRIAL*CONTEXT interaction on a cluster of data points extending from -300 to -190 ms and involving the $ROI_{Central\_1\text{-}2}$ locations (cluster thresholded at $p < .05$; Figure 10.A).

We did not observe any effect of conflict expectation on motor activity in congruent trials. RLPs were comparable in the MCB and MIB contexts, whether recorded in the $HEMI_{Ipsi\text{-}to\text{-}Resp}$ ($p = .17$; Figure 10.B, C and D) or the $HEMI_{Contr\text{-}to\text{-}Resp}$ ($p = .09$). In contrast, we observed significant differences in RLPs between the two block types for the $HEMI_{Ipsi\text{-}to\text{-}Resp}$ in incongruent trials. As such, ipsilateral activity was significantly larger in MIBs than in MCBs ($p = .002$); such a context-dependent effect was not present for the $HEMI_{Contra\text{-}to\text{-}Resp}$ ($p = .96$).

Hence, the RLP data suggest that conflict expectation does not reduce the impact of incongruent stimuli on motor activity. On the contrary, activation of the ipsilateral motor cortex became larger in the MIBs than in the MCBs following incongruent signals. Therefore, the higher accuracy of subjects in incongruent trials of MIBs cannot be accounted for by a specific reduction in the activation of inappropriate motor representations. Contrariwise, these cortical representations were more active in MIBs than MCBs.

Altogether, our results confirm that subjects are better at resolving conflict when it is expected in advance and that this enhancement is associated with a higher midfrontal theta activity. Surprisingly, the SSVEP and RLP data point out that these changes occur in parallel with a reduced filtering of information at the visual level and increased inappropriate activations at the motor level. Hence, conflict expectation seems to recruit control processes that augment the tolerance for inappropriate motor activations (rather than on processes that downregulate their amplitude), allowing them to occur without leading to the selection of an incorrect response. This mechanism might contribute to the enhancement of accuracy, but may restrain decision speed.

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Figure 10 about here

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729

730 ***Methodological note***

731 Given the experimental design, congruent and incongruent trials could be either minority
732 (in MIB and MCB, respectively) or majority (in MCB and MIB, respectively). This means that
733 averages were computed on a varying amount of trials. To account for this possible bias when
734 analyzing the RLP data (not applicable for SSVEP and ΔSpectAmp data given the absence of
735 factor TRIAL for these dependent variables), additional analyses were run using an equalized
736 number of epochs across conditions (set based on the condition involving the smallest amount
737 of trials). Importantly, these analyses provided the same RLP results as those presented using
738 the full set of trials.

739 Another point of consideration for the RLP analysis concerns the time window used for
740 baseline correction (*i.e.*, -700 to -500 ms with respect to the response). As such, because the RT
741 varied between conditions (and between subjects), this time window could overlap with the last
742 second of the flickering period, either in part (*i.e.*, in the case of RTs longer than 500 ms), or in
743 total (*i.e.*, for RTs shorter than 500 ms). In other words, the baseline overlapped with the period
744 during which SSVEPs were induced. To control for this potential bias, we tested different time
745 windows for baseline correction (*i.e.*, - 800 to -600 ms, -900 to -700 ms), getting back in time
746 with respect to the motor response, and thus increasing the fraction of the time window
747 overlapping with the flickering period. Again, we obtained the exact same results as in the main
748 analysis, indicating the robustness of the effects reported.

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DISCUSSION

The primary goal of the present study was to investigate the impact of conflict expectation on selective attention in the visual cortex and on action selection in the motor cortex. We recorded SSVEPs and RLPs during an Eriksen Flanker task where conflict was either highly predictable (MIBs) or very unlikely (MCBs). Besides, we also considered midfrontal theta activity during the fixation period as a marker of cognitive control.

Midfrontal theta activity was higher in MIBs than in MCBs, indicating the engagement of control processes recruited in anticipation of conflict: these are probably responsible for the fact that subjects responded more accurately in incongruent trials when conflict was expected. Notably, this enhanced accuracy in MIBs occurred at the cost of speed, as subjects became slower to respond in congruent trials. Yet, surprisingly, visuomotor activity was less finely tuned in MIBs. As such, target-related SSVEPs were smaller while peripheral flanker-related SSVEPs were higher in MIBs than MCBs, and RLPs were larger in the ipsilateral motor cortex during conflicting trials of MIBs. These findings suggest that conflict expectation recruits cognitive control processes that augment the tolerance for inappropriate visuomotor activations, allowing them to occur without leading to the selection of an incorrect action.

As expected, movement initiation was associated with a prominent activity in the motor cortex contralateral to the responding hand. Indeed, contralateral RLPs became larger than ipsilateral ones from -150 ms preceding movement onset, consistent with the literature (Nguyen et al., 2014; Noorbaloochi et al., 2015). However, activity in the ipsilateral motor cortex was surprisingly pronounced in our task, even in congruent trials. In fact, congruent trials were associated with an initial boost of ipsilateral activity, which surpassed contralateral activity from about -350 to -200 ms before movement onset, regardless of the context or of the responding hand. Albeit not highlighted in the past, this effect seems also present in previous studies using flanker tasks (Paasmtra and Seiss, 2005; Klein et al., 2014). Why should the

ipsilateral (non-selected) motor cortex become so active soon after the imperative signal, even in the absence of conflict? One possibility is that it has to do with the distribution of inhibitory influences directed at motor representations during action preparation (Derosiere, 2018; Duque et al., 2014, 2017). Indeed, these influences are predominantly directed at selected representations (Quoilin and Derosiere, 2015; Vassiliadis et al., 2018) and only to a smaller extent at non-selected ones. Given that EEG potentials result from the summation of excitatory and inhibitory processes (Muthukumaraswamy et al., 2013), one may assume that the higher activity initially observed in the ipsilateral motor cortex is due to the lower level of preparatory inhibition directed at this (non-selected) area, compared to the selected, contralateral one.

Conflict expectation altered the strength of ipsilateral motor activity in incongruent trials but not in congruent ones. Indeed, the RLP data revealed a comparable level of motor activity for congruent trials, whether performed in MIBs or MCBs. Conversely, incongruent trials were associated with a higher activity in the ipsilateral motor cortex in MIBs compared to MCBs. This indicates that inappropriate motor activity following conflicting signals was larger when conflict had been anticipated compared to when it occurred unexpectedly. Importantly, these neural responses were obtained in trials where subjects turned out to select the correct action. Hence, the (high) ipsilateral activity observed in MIBs must have remained nevertheless "below threshold" given that it did not lead to the selection of an inappropriate response. This finding suggests that conflict expectation is associated with an extension of the distance-to-threshold in MIBs. Such an extension may be implemented by a rise in the selection threshold or by a decrease in the level at which the motor cortex starts to accumulate neural activity (*i.e.*, the starting point; Herz et al., 2017; Kim et al., 2017). In fact, several lines of evidence suggest that conflict expectation could downregulate the starting point of neural accumulation. Indeed, previous studies showed that the motor cortex exhibits a drop of baseline activity when task requirements constrain subjects to focus on decision accuracy (Pastotter et al., 2011; Thura et

al., 2016) – *i.e.*, as when conflict occurrence is frequent. Along the same line, recent TMS studies revealed that corticospinal excitability is globally suppressed when conflict is highly expected compared to when it is unlikely (Klein et al., 2014; Duque et al., 2016). Most noticeably, this global suppression has been evidenced at the time of the imperative signal, consistent with a downregulation of the starting point of neural accumulation. Unfortunately, the presence of such a shift cannot be detected in the current EEG dataset as pre-stimulus signals are exploited to correct RLPs for baseline fluctuations, annihilating any putative differences in baseline activity between the different conditions (Maess et al., 2016).

At the behavioral level, an enlarged distance-to-threshold is thought to produce a shift in speed-accuracy tradeoff, favoring accuracy over speed, as revealed by studies using computational modeling of behavioral data (Forstmann et al., 2010; Hauser et al., 2017; Thura and Cisek, 2017). Accordingly, here (and in Burle et al., 2016), subjects were more accurate in incongruent trials of MIBs than MCBs but showed longer RTs in easy, congruent trials. We recognize that one would assume a shift in speed-accuracy tradeoff to induce a global reduction of decision speed, altering RTs regardless of the trial type, while here (and in Burle et al., 2016), the deceleration was only present in congruent trials. This may be due to the fact that subjects had to respond under a fixed deadline. Given that RTs are long by default in incongruent trials (*i.e.*, even in MCBs), the imposed time limit may have left little space for a further slow-down in MIBs. Future studies should investigate the effect of conflict expectation on decision speed in the absence of temporal constraints.

Incongruent trials were associated with a particularly low level of activity in the ipsilateral motor cortex when conflict had not been expected in advance. As such, inappropriate motor activity was less pronounced in MCBs than in MIBs, as explained above. Moreover, the ipsilateral motor activity elicited by incongruent signals in MCBs was also less pronounced than that recorded in the same context following congruent signals. Hence, when conflict

827 occurred unexpectedly, inappropriate motor activity was strongly restrained. One possibility is
828 that conflict detection in MCBs led to the recruitment of online control processes suppressing
829 inappropriate activations. Such an online inhibitory mechanism has been proposed to operate
830 during action reprogramming, as when sudden environmental changes call for the suppression
831 of habitual motor responses (Mars et al., 2009; Neubert et al., 2010), or when unexpected
832 obstacles require to abort initially-planned movement trajectories (Archambault et al., 2011).
833 Our results suggest that such process may also assist action selection in front of unexpected
834 conflict.

835 Interestingly, the efficiency of online control processes has been shown to depend on the
836 degree of visual attention directed at goal-relevant information (Reichenbach et al., 2014). Our
837 data are coherent with these previous findings. As such, we observed that the level of attention
838 directed towards the target location was stronger in MCBs than in MIBs, while attention to
839 goal-irrelevant locations was reduced in the former than in the latter context. A sharper
840 attentional focus in MCBs may have allowed subjects to limit the impact of incongruent
841 flankers on motor activity when they appeared unexpectedly. Such a control system may be
842 particularly prominent in contexts where conflict is rare, as it allows to limit the impact of
843 conflict when it occurs, without slowing down responses otherwise.

844 Hence, control strategies seem to be adapted to favor success in the most common type of
845 trials in a given context. A low distance-to-threshold combined with substantial online control
846 is the most efficient strategy in MCBs: it allows fast responses on most (congruent) trials while
847 ensuring a reasonable level of accuracy when conflict eventually occurs. In contrast, a proactive
848 control system extending the distance-to-threshold is the most efficient strategy in MIBs: it
849 allows accurate responses in most (incongruent) trials and the cost in terms of speed merely
850 concerns a minority of (congruent) trials.

Finally, another interesting finding concerns the involvement of the dominant motor cortex in conflict resolution. In the presence of conflict, neural activity was higher in the left (dominant) motor cortex than in the right (non-dominant) one, regardless of the responding hand. This finding suggests that the left motor cortex contributes to a higher extent to the resolution of visuomotor conflict than the right one. Consistently, control processes underlying the execution of visually-guided movements are asymmetrically organized in the human brain with a superiority of the left cerebral hemisphere (Bardi et al., 2012; Frey et al., 2008; Haaland et al., 2004). Our findings indicate that the predominance of the left motor cortex goes beyond motor control processes, and extends to motor decision-making. Moreover, because this effect was observed in both MCBs and MIBs, the dominance of the left hemisphere seems to concern conflict resolution regardless of the actual control strategy recruited to ensure appropriate behavior.

In conclusion, the comparison of visuomotor activity in MCBs and MIBs suggests that conflict resolution relies on distinct control strategies depending on the level of conflict expectation. When most trials are conflicting, the distance-to-threshold may be generally enlarged in a proactive way, allowing inappropriate visuomotor activity to occur without having it cause incorrect responses, hence favoring accurate performance on most trials. Conversely, when conflict is rare, the distance-to-threshold may be shorter, allowing fast responses on most (congruent) trials; in this context, conflict resolution seems to rather rely on a sharp attentional focus on the target with a low attention towards goal-irrelevant locations and on online inhibition of inappropriate motor activity, preventing neural accumulation from reaching the (low) selection threshold.

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LEGENDS

Figure 1: Task design. A. Trial types. Subjects were asked to perform congruent (*upper panel*) and incongruent (*lower panel*) trials requiring left (*left panel*) or right (*right panel*) finger responses according to an imperative stimulus consisting of a central arrow (target) surrounded by two irrelevant arrows on each side (flankers). **B.** Time course of a typical trial. Each trial started with the presentation of five black squares remaining on the screen for 7000 ms (*top left*). Then, the imperative stimulus appeared (*top right*), indicating the required response (right key-press in current example). Once a response was provided (or after 700 ms), a mask appeared and remained on the screen for an interval of 1200 ms (*bottom right*). A feedback score was then displayed for 1500 ms depending on the subject RT and accuracy (*bottom left*). **C.** Block types. The experiment involved two block types including either a majority of congruent trials (MCB; *left*) or a majority of incongruent trials (MIB; *right*). Conflict expectation was highest in the latter block type. **D.** SSVEP procedure. In half of the blocks, the stimuli were slightly shifted to the left (*left panel*) whereas they were slightly shifted to the right in the other blocks (*right panel*). The target square ($Target_{Sq}$) appeared on the left of the fixation cross in left-shifted stimuli and on the right of it in right-shifted stimuli; it was flickering at 16.6 Hz. The most central flanker square (Flanker-C_{Sq}) was flickering at 12.5 Hz; it was always the one located on the other side of the fixation point. The three more peripheral flanker squares (Flanker-P_{Sq}) were flickering at 14.2 Hz.

Figure 2: EEG data processing steps. A. Attention epochs - SSVEP. (1) For each subject, multiple Z-scored spectra were obtained (*i.e.*, in 4 conditions and 64 electrodes). Typical single-subject spectra are represented, showing three SSVEP peaks at 12.5, 14.2 and 16.6 Hz. (2) The spectra obtained at electrodes of a posterior region of interest (ROI_{Post}) were exploited to compute linear channel maps. (3) A cluster-based statistical analysis was applied on the maps

to test for any significant effect of the factors of interest (*i.e.*, HEMISPHERE and CONTEXT) on the spectral amplitude among the frequency and scalp location dimensions. **B.** Selection epochs - RLP. (1) For each subject, multiple response-locked potentials were obtained (in $\mu V/m^2$; *i.e.*, in 16 conditions and 64 electrodes). Typical single-subject potentials are represented. (2) The potentials obtained at electrodes of a central ROI ($ROI_{Central}$) were exploited to compute channel maps. (3) A cluster-based statistical analysis was applied on the maps to test for any significant effect of the factors of interest (*e.g.*, TRIAL [congruent, incongruent], CONTEXT [MCB, MIB], *etc*) on the potential amplitude among the time and scalp location dimensions.

Figure 3: Accuracy (*upper traces*; **A-C**) **and RT** (*lower traces*; **D-F**) **data (mean ± SE). A&D.** The HAND factor significantly impacted the accuracy and RT data. Green and blue colors represent data obtained for left and right hand responses, respectively. Both trial types and contexts are pooled together. **B&E.** The TRIAL factor had a significant influence on the accuracy and RT data. Both hands and contexts are pooled together. **C&F.** The TRIAL*CONTEXT interaction was significant. Both hands are pooled together. *: Significant difference at $p < .05$.

Figure 4: Effect of conflict expectation on midfrontal theta activity. A. The cluster-based statistical analysis revealed that ΔSpectPower, a marker of theta activity due to conflict expectation, was significantly different from 0 for a cluster of data points in the theta range. **B.** Grand-average TF maps were obtained for the Fpz (top), Fz (middle) and Cz (bottom) electrodes. For illustrative purposes, maps were resampled by multiplying temporal and frequency resolutions by a factor of 10. The rectangle delineated by black dotted lines highlights the significant cluster on each map: note the significantly higher ΔSpectPower for the

midfrontal Fz electrode specifically (absence of effect for the two other electrodes). **C.** Grand-average topography were obtained using the time-frequency boundaries of the detected cluster to extract the values at each electrode: [+4700 ms +5400 ms] / [6 8 Hz]. **D.** Post-hoc results show the larger ΔSpectPower for Fz compared to Fpz and Cz. Time-frequency boundaries used to extract the cluster-level average values in each subject are the same as in *C.* Bar graphs represent group-level mean ± SE. *: Significant difference at $p < .05$.

Figure 5: Effect of the factor HEMISPHERE on SSVEPs. **A.** The cluster-based statistical analysis revealed a significant main effect of HEMISPHERE on two clusters of data points, highlighted in red. **B.** Effect of HEMISPHERE at the Flanker-C_{Sq} frequency. *Top*: Grand-average channel maps as obtained for $HEMI_{Contra\text{-}to\text{-}Target}$ (left) and $HEMI_{Ipsi\text{-}to\text{-}Target}$ (right; ipsilateral and contralateral to the Flanker-C_{sq}, respectively). The ROI_{Post} locations (2-5) showing a significant HEMISPHERE effect are comprised in the rectangles delineated by the black dotted lines. *Bottom left:* Grand-average frequency spectra (all electrodes composing the cluster pooled together) as obtained for the $HEMI_{Contra\text{-}to\text{-}Target}$ (solid line) and $HEMI_{Ipsi\text{-}to\text{-}Target}$ (dashed line). The gray rectangle highlights the frequency window of statistical significance. *: Significant difference at $p < .05$. *Bottom right:* Grand-average topographies at 12.5 Hz for left- and right-shifted stimuli (left and right topographies, respectively). The electrodes composing the detected cluster are highlighted by small black stars. **C.** Same as B. for the $Target_{Sq}$ frequency.

Figure 6: Effect of the factor CONTEXT on SSVEPs. A. The cluster-based statistical analysis revealed a significant main effect of CONTEXT on two clusters of data points, highlighted in red. **B.** SSVEP amplitude in MCB (orange) and MIB (red) blocks. *Top left*: Grand-average channel maps as obtained for MCBs and MIBs. The ROI_{Post} locations (1-3)

showing a significant effect of the factor CONTEXT at the Flanker-P_{Sq} frequency are comprised in the rectangles delineated by the black dotted lines. *Top right:* Grand-average frequency spectra (all electrodes composing the cluster pooled together) as obtained for the MCBs (orange) and MIBs (red). Note the higher Flanker-P_{Sq}-related SSVEPs in MIBs compared to MCBs. The gray rectangle highlights the frequency window of statistical significance. *: Significant difference at $p < .05$. *Bottom:* Grand-average topographies at 14.2 Hz for left- and right-shifted stimuli (left and right topographies, respectively). The electrodes composing the detected cluster are highlighted by small black stars.

Figure 7: Effect of the HEMISPHERE*CONTEXT*TIME interaction on SSVEPs. **A.** The cluster-based statistical analysis revealed a significant HEMISPHERE*CONTEXT*TIME interaction on a cluster of data points, highlighted in red. **B.** At $Stage_{Early}$. *Top*: Grand-average channel maps as obtained for $HEMI_{Contra\text{-}to\text{-}Target}$ (left) and $HEMI_{Ipsi\text{-}to\text{-}Target}$ (right), in MCBs (top) and MIBs (bottom). The ROI_{Post} locations (4-5) showing a significant HEMISPHERE*CONTEXT*TIME interaction are comprised in the rectangles delineated by the black dotted lines. *Bottom left:* Grand-average frequency spectra as obtained for the $HEMI_{Contra\text{-}to\text{-}Target}$ (solid line) and $HEMI_{Ipsi\text{-}to\text{-}Target}$ (dashed line), in MCBs (orange) and MIBs (red). The frequency spectra measured at the electrodes composing the detected cluster were averaged together. The gray rectangle highlights the frequency window of statistical significance. *: Significant difference at $p < .05$. *Bottom right:* Grand-average topographies at 16.6 Hz for left- and right-shifted stimuli (left and right topographies, respectively). The electrodes composing the detected cluster are highlighted by small black stars. **C.** Same as *B.* for the $Stage_{Late}$. *: Significant difference at $p < .05$.

Figure 8: Effect of the factor HEMISPHERE on RLPs. **A.** The cluster-based statistical analysis revealed a significant main effect of the HEMISPHERE factor on two clusters of data points, highlighted in red. **B.** *Top panel*: Grand-average channel maps as obtained for $HEMI_{Contra\text{-}to\text{-}Resp}$ (left) and $HEMI_{Ipsi\text{-}to\text{-}Resp}$ (right). The $ROI_{Central}$ locations showing a significant effect of HEMISPHERE are comprised in the rectangles delineated by the black dotted lines. *Bottom-left panel:* Grand-average RLP waveforms as obtained for the $HEMI_{Contra\text{-}to\text{-}Resp}$ (solid line) and $HEMI_{Ipsi\text{-}to\text{-}Resp}$ (dashed line). The RLPs measured at the electrodes composing the two detected clusters were averaged separately; that is, $ROI_{Central\_1}$ and $ROI_{Central\_2}$ were exploited to compute the left segment of the RLP (from - 500 ms to -150 ms) while the averaging for the right segment also involved $ROI_{Central\_3}$ (from -150 to -50 ms). The two gray rectangles highlight the time windows of statistical significance. *: Significant difference at $p < .05$. *Bottom-right panel:* Grand-average topographies at -250 ms and -100 ms (left and right topographies, respectively) for left hand responses. The electrodes composing each detected cluster are highlighted by small black stars.

Figure 9: Effect of the HEMISPHERE*HAND*TRIAL interaction on RLPs. **A.** The cluster-based statistical analysis revealed a significant main effect of the HEMISPHERE*HAND*TRIAL interaction on a cluster of data points, highlighted in red. **B.** *Left panel*: Grand-average channel maps as obtained for congruent trials, for left (top row) and right (bottom row) hand responses, in $HEMI_{Contra\text{-}to\text{-}Resp}$ (left column) and $HEMI_{Ipsi\text{-}to\text{-}Resp}$ (right column). The $ROI_{Central}$ location showing a significant HEMISPHERE*HAND*TRIAL interaction is comprised in the rectangles delineated by the black dotted lines. *Right panel*: Same as *B. Left panel* for incongruent trials. **C.** *Left panel:* Grand-average RLP waveforms as obtained for congruent (left column) and incongruent (right column) trials, for left (top row; green) and right (bottom row; blue) responses, in the $HEMI_{Contra\text{-}to\text{-}Resp}$ (solid lines) and

HEMI$_{Ipsi\text{-}to\text{-}Resp}$ (dashed lines). The RLP waveform measured at the electrode composing the detected cluster was extracted for each condition. The gray rectangle highlights the time window of statistical significance. *: Significant difference at $p < .05$. *Right panel:* The same RLP waveforms as the ones represented in *C. Left panel* were exploited to highlight the significant differences in RLP amplitude for left and right responses in incongruent trials. RLPs obtained in the HEMI$_{Contra\text{-}to\text{-}Resp}$ and HEMI$_{Ipsi\text{-}to\text{-}Resp}$ are represented at top and bottom rows, respectively. **D.** Grand-average topographies for congruent (left; obtained at - 250 ms) and incongruent (right; at - 200 ms) trials. For each trial type, topographies for both hand responses are represented. The electrode composing the detected cluster is highlighted by small black stars.

Figure 10: Effect of the HEMISPHERE*TRIAL*CONTEXT interaction on RLPs. **A.** The cluster-based statistical analysis revealed a significant main effect of the HEMISPHERE*TRIAL*CONTEXT interaction on a cluster of data points, highlighted in red. **B.** *Left panel*: Grand-average channel maps as obtained for congruent trials, for MCB (top row) and MIB (bottom row) contexts, in HEMI$_{Contra\text{-}to\text{-}Resp}$ (left column) and HEMI$_{Ipsi\text{-}to\text{-}Resp}$ (right column). The ROI$_{Central}$ location showing a significant HEMISPHERE*TRIAL*CONTEXT interaction is comprised in the rectangles delineated by the black dotted lines. *Right panel*: Same as *B. Left panel* for incongruent trials. **C.** *Left panel:* Grand-average RLP waveforms as obtained for congruent (left column) and incongruent (right column) trials, for MCB (top row; orange) and MIB (bottom row; red) contexts, in the HEMI$_{Contra\text{-}to\text{-}Resp}$ (solid lines) and HEMI$_{Ipsi\text{-}to\text{-}Resp}$ (dashed lines). The RLP waveforms measured at the electrodes composing the detected cluster were averaged together for each condition. The gray rectangle highlights the time window of statistical significance. *: Significant difference at $p < .05$. *Right panel:* The same RLP waveforms as the ones represented in *C. Left panel* were exploited to highlight the

significant differences in RLP amplitude in the $HEMI_{Ipsi\text{-}to\text{-}Resp}$ between MCB and MIB contexts in incongruent trials. RLPs obtained in the $HEMI_{Contra\text{-}to\text{-}Resp}$ and $HEMI_{Ipsi\text{-}to\text{-}Resp}$ are represented at top and bottom rows, respectively. **D.** Grand-average topographies obtained at -230 ms for congruent (left) and incongruent (right) trials. For each trial type, topographies for both hand responses and both contexts are represented. The electrodes composing the detected cluster are highlighted by small black stars.