Published in final edited form as:

J Cogn Neurosci. 2009 August ; 21(8): 1461–1472. doi:10.1162/jocn.2009.21136.

Anticipating conflict facilitates controlled stimulus-response selection

Ángel Correa^{1,2}, Anling Rao², and Anna C. Nobre²

¹Departamento de Psicología Experimental, Universidad de Granada, Spain

²Department of Experimental Psychology, University of Oxford, UK

Abstract

Cognitive control can be triggered in reaction to previous conflict, as suggested by the finding of sequential effects in conflict tasks. Can control also be triggered proactively by presenting cues predicting conflict ('proactive control')? We exploited the high temporal resolution of event-related potentials (ERPs) and controlled for sequential effects to ask whether proactive control based on anticipating conflict modulates neural activity related to cognitive control, as may be predicted from the conflict-monitoring model. ERPs associated with conflict detection (N2) were measured during a cued flanker task. Symbolic cues were either informative or neutral with respect to whether the target involved conflicting or congruent responses. Sequential effects were controlled by analysing the congruency of the previous trial. The results showed that cuing conflict facilitated conflict resolution and reduced the N2 latency. Other potentials (frontal N1 and P3) were also modulated by cuing conflict. Cuing effects were most evident after congruent than after incongruent trials. This interaction between cuing and sequential effects suggests neural overlap between the control networks triggered by proactive and reactive signals. This finding clarifies why previous neuroimaging studies, in which reactive sequential effects were not controlled, have rarely found anticipatory effects upon conflict-related activity. Finally, the high temporal resolution of ERPs was critical to reveal a temporal modulation of conflict detection by proactive control. This novel finding suggests that anticipating conflict speeds up conflict detection and resolution. Recent research suggests that this anticipatory mechanism may be mediated by pre-activation of the ACC during the preparatory interval.

Keywords

cognitive control; cuing conflict; event-related potential (ERP); N2; error-related negativity (ERN); anterior cingulate cortex (ACC)

INTRODUCTION

Most classic models of cognition posit a control system that selects stimuli and responses according to task goals (e.g., Atkinson & Shiffrin, 1968; Kahneman, 1973; Norman & Shallice, 1986). This system is engaged under conflicting situations, such as when

simultaneously occurring events call for multiple and incompatible responses (Eriksen & Eriksen, 1974); and after negative behavioural outcomes, such as errors (see Ridderinkhof, Ullsperger, Crone, & Nieuwenhuis, 2004, for a review). After conflict or errors, behavioural measures reveal a more deliberate mode of responding ('sequential effects', Gratton, Coles, & Donchin, 1992; 'post-error slowing', Rabbitt, 1966).

Neural models of conflict monitoring (e.g., Botvinick, Braver, Barch, Carter, & Cohen, 2001) posit that the anterior cingulate cortex (ACC) detects conflict, and recruits dorsolateral prefrontal cortex (DLPFC) to bias stimulus-response selection through top-down signals. Neuroimaging research has confirmed increased ACC activation by conflict, followed by decreased ACC activation on the subsequent conflicting trial; suggesting successful conflict reduction by an increased attentional set (Botvinick, Nystrom, Fissell, Carter, & Cohen, 1999; Kerns et al., 2004).

Conflict monitoring is triggered in reaction to previous conflict ('reactive control'), as suggested by the finding of sequential effects in conflict tasks (Gratton, Coles, & Donchin, 1992). Gratton and colleagues used a flanker task (Eriksen & Eriksen, 1974) and found that the conflict effect (RT difference between incongruent and congruent conditions) was reduced when the previous trial was incongruent rather than congruent. However, top-down control is not only triggered reactively but also proactively (Logan & Zbrodoff, 1982). Logan and Zbrodoff (1982) induced 'proactive control' by presenting cues predicting conflict in a Stroop task (Stroop, 1935). The results showed that the anticipation of an incongruent trial reduced the conflict effect. Thus, proactive control is analogous to attentional orienting more generally, during which expectations about a particular event attribute trigger top-down biases of relevant stimulus/response representations (Kastner & Ungerleider, 2000).

Although the conflict-monitoring model was primarily based on reactive control (Botvinick, Braver, Barch, Carter, & Cohen, 2001), a clear prediction can also be made for proactive control. Behavioural facilitation of conflict resolution by proactive control should be associated with modulations of conflict-related neural activity (e.g., decreased ACC activity). However, neuroimaging studies using conflict-predicting cues have led to inconclusive results (Fassbender, Foxe, & Garavan, 2006; Luks, Simpson, Dale, & Hough, 2007; Luks, Simpson, Feiwell, & Miller, 2002; Sohn, Albert, Jung, Carter, & Anderson, 2007). The scarce evidence showing that proactive control modulates conflict processing could be explained by two factors: (1) the limited temporal resolution of hemodynamic measures or (2) the masking of proactive control effects due to modulatory effects caused by reactive control. None of these studies manipulating proactive control considered the effect of previous trial congruency. If proactive and reactive control share neural mechanisms, then the effects of proactive control would be most evident when reactive control is low (i.e. after congruent rather than incongruent trials).

Here, we (1) exploited the high temporal resolution of ERPs, and (2) controlled for the effects of reactive control in a cued flanker task to ask whether proactive control modulates neural activity related to conflict. Previous research using conflict tasks and ERPs has identified two frontal potentials related to cognitive control. A negative deflection is

observed after stimuli that carry incongruent versus congruent response tendencies (N2) (Kopp, Rist, & Mattler, 1996), as well as after an incorrect response (error-related negativity – ‘ERN’ or ‘Ne’) (Falkenstein, Hohnsbein, Hoormann, & Blanke, 1990; Gehring, Goss, Coles, Meyer, & Donchin, 1993). The ACC is thought to constitute an important source to both the N2 and ERN (Debener et al., 2005; van Veen & Carter, 2002), which, respectively, have been interpreted as indices of conflict detection (van Veen & Carter, 2002) and error detection (reviewed by Falkenstein, Hoormann, Christ, & Hohnsbein, 2000).

The central hypothesis of this study was that the anticipation of conflict should modulate control-related potentials. Two ERP analyses were conducted on control-related ERPs: stimulus-locked and response-locked. The stimulus-locked analysis tested whether conflict processing, as indexed by the N2 potential, was attenuated by cuing conflict. Additionally, this analysis allowed us to explore whether proactive and reactive control operate through a common attentional system, as suggested by their analogous behavioural effects (Gratton, Coles, & Donchin, 1992; Logan & Zbrodoff, 1982). We compared modulations of stimulus-locked potentials by cuing versus by previous conflict processing. If their neural mechanisms overlap, proactive and reactive control should interact in their modulation of conflict-related neural processing. Stronger effects of proactive control should hence be expected under low versus high reactive control. On the other hand, if proactive and reactive control involve independent mechanisms, we should observe dissociable modulations of conflict processing.

The response-locked analysis tested whether error-related processing indexed by the ERN and the ensuing ‘error positivity’ (Pe) (Falkenstein, Hohnsbein, Hoormann, & Blanke, 1990, 2000) were modulated by cuing conflict. High time pressure for responding was imposed to ensure reliable numbers of error trials for ERP analysis (e.g., Nieuwenhuis et al., 2006; Ullsperger, Bylsma, & Botvinick, 2005).

METHODS

Participants

Twenty participants from the University of Oxford (aged 19-49, 9 female) took part voluntarily in the experiment. Data from 1 participant were rejected due to excessively low accuracy during task performance (58% correct). The experimental methods were non-invasive and had ethical approval from the University of Oxford.

Stimuli and Task

Participants completed a cued flanker task under high time pressure. They were to respond according to the direction pointed by a central arrow, while ignoring the direction of the flanking arrows. The target was preceded by a cue stimulus, which was either informative or neutral with respect to the congruency between the central and flanking arrows. Informative cues were 100% predictive (‘cued’ condition). A green checkmark indicated that the central and flanking arrows would be congruent. A red cross indicated they would be incongruent. A yellow question mark provided no prediction about congruency (‘neutral’ condition). A sufficiently long interval was used between the cue and the flanker array (1000-1500 ms) to

enable the implementation of endogenously generated expectations about the upcoming stimulus congruency (e.g., see Gratton, Coles, & Donchin, 1992; Monsell, 2003; Müller & Rabbitt, 1989). The cue stimulus subtended $1.2^\circ \times 1.2^\circ$. Target arrays consisted of five white arrows ($1.4^\circ \times 1^\circ$ each) appearing in a row and centred on the fixation point (a gray dot with 0.3° diameter). The direction of the central arrow (left or right) could be the same (congruent) or different (incongruent) from that of the flankers. All flankers pointed in the same direction.

Figure 1 illustrates the main events of the task for the four incongruent conditions used to compare proactive cuing and reactive sequential effects. These included cuing (cued, neutral) and congruency of the target on the previous trial ('previous congruency': congruent, incongruent).

Each trial began with a fixation point presented centrally for a random interval that ranged between 500 and 1000 ms. The cue was then presented centrally for 100 ms and followed by a blank display for a random interval of 1000-1500 ms. The target array then appeared, and remained until the participant responded or a maximum deadline elapsed. The deadline was set at 450 ms, and was adjusted across blocks to maintain a good level of performance that was below ceiling (around 70%). The deadline was increased by 50 ms if the error rate was above 35% in the preceding block, or was decreased by 50 ms if it was below 25%. The participant had to press the 'z' key with the left index finger or the 'm' key with the right index finger, according to the direction pointed by the central arrow. After a timely response or the deadline, there was a blank display of 700 ms. If participants had failed to respond within the deadline, a visual feedback 'faster!' then appeared for 500 ms. Following a timely response or the feedback, a blank display of 500 ms preceded the next trial.

The experiment included 3 practice blocks plus 42 experimental blocks. Each block consisted of 16 trials, including 2 trials of each type according to the type of cuing (cued, neutral), flanker (congruent, incongruent), and direction of the central arrow (left, right). The proportion of congruent and incongruent targets was .5. On average, half of current trials were preceded by congruent or incongruent trials.

EEG recording

The EEG recording was performed in an electrically shielded room, using Ag/AgCl electrodes mounted on an elastic cap and distributed along 34 scalp sites according to the 10-20 International system (AEEGS, 1991) using NuAmp amplifiers (Neuroscan, El Paso, TX). The montage included 6 midline sites (FZ, FCZ, CZ, CPZ, PZ and OZ) and 14 sites over each hemisphere (FP1/FP2, F7/F8, F3/F4, FT7/FT8, FC3/FC4, T7/T8, C3/C4, TP7/TP8, CP3/CP4, P7/P8, P3/P4, PO7/PO8, PO3/PO4 and O1/O2). Additional electrodes were used as ground and reference sites, and for recording the electrooculogram (EOG). All electrodes were referenced to the right mastoid during the recording and were algebraically re-referenced off-line to calculate the average of the right and left mastoids. Eye movements were monitored by horizontal and vertical EOG bipolar recordings with electrodes placed around the eyes. The EEG was amplified with a low-pass filter of 300 Hz and digitized at a sampling rate of 1000 Hz.

ERP analysis

The continuous EEG was filtered offline with a 40-Hz low-pass filter. Separate epochs were constructed for targets (between –100 and 600 ms relative to target onset) and responses (between –600 and 700 ms relative to response onset). Their respective baselines consisted of a 100-ms epoch before target onset, and a 50-ms epoch between –100 and –50 ms relative to response onset. Epochs in which an eye blink or eye movement occurred were rejected on the basis of large deflections ($\pm 50\mu\text{V}$) in the HEOG or VEOG electrodes. Epochs with large signal drift were also removed, on the basis of large deflections ($\pm 100\mu\text{V}$) in any channel.

An initial analysis compared ERPs triggered by congruent versus incongruent targets, in order to replicate the well established effects of conflict on the N2 potential. The analysis of main interest followed, which tested the effects of proactive control upon *conflict* processing, and compared them with the effects of reactive control. Accordingly, only ERPs elicited by the conflict-carrying incongruent target conditions were included. Epochs were averaged according to the four conditions defined by cuing (cued, neutral) and previous congruency (congruent, incongruent). Only incongruent targets with correct responses were analysed. Identifiable target-related potentials were analysed at electrode locations and temporal windows where they were most evident according to the segmentation analysis performed with Cartool software (see below: ‘Topographical Analyses’). Target-locked waveforms averaged across participants are shown in Figure 3 (top). The first negative deflection peaked at 110 ms over frontal electrodes and was referred to as ‘frontal N1’ (N1f). According to the segmentation analysis, the N1f occurred around 90-130 ms, and extended from frontal to centroparietal electrodes with maximal intensity over the left frontal scalp (Figure 3 bottom). The N1f was therefore analysed during 90-130 ms over frontal to centroparietal electrode positions (F3/Z/4, FC3/Z/4, C3/Z/4, CP3/Z/4). The P1 overlapped temporally with the N1f, peaking at 120 ms, and was maximal over occipital electrodes (O1/2, PO3/4, PO7/8). N1 peaked at 170 ms and was also maximal over occipital electrodes (O1/2, PO3/4, PO7/8). P1 and N1 were analysed during 110-130 and 160-180 ms over three occipital positions (O1/2, PO3/4, PO7/8). The N2 peaked at about 305 ms over frontal electrodes, and was analysed during 290-330 ms at F3/Z/4 and FC3/Z/4. The P3 peaked at 425 ms and was broadly distributed over the central scalp. The P3 was analysed during 360-460 ms at FC3/Z/4, C3/Z/4, CP3/Z/4, P3/Z/4.

An analysis of response-related ERPs focused on whether cuing conflict modulated *error* processing. The epochs were averaged separately for errors and correct responses during incongruent trials, according to the cuing conditions (cued, neutral). Responses to congruent targets led to insufficient numbers of observations on the error condition and hence were not analysed. Likewise, conditions with previous congruent and incongruent targets were collapsed to gain statistical power.

Error analyses followed the same approach as for targets, using time periods defined by topographical segmentation and the electrodes showing the maximal distribution of potentials. Around the time of response, ERPs elicited by errors contained an ERN that peaked at about 20 ms after the response (see Figure 4 top panel)¹ and was focally

distributed over frontocentral electrodes (bottom Figure 4, 'map 2'). This was followed by positive-going potentials, similar to the error positivity (Pe), which separated into two different topographical states (maps 4 and 5). ERPs elicited by correct responses were characterised by a positive potential, the 'correct positivity' (Pc), at the same time range as the ERN, which was distributed over central electrodes (bottom Figure 4, 'map 3'). The Pc was then followed by continued positive potentials subdivided into two topographical states. The ERN was analysed at 0-40 ms over frontal and frontocentral electrodes (F3/Z/4, FC3/Z/4). The Pe was analysed over frontal to central electrodes (F3/Z/4, FC3/Z/4, C3/Z/4) at two epochs: early Pe (50-110 ms, map 4) and late Pe (250-290 ms, map 5) (van Veen & Carter, 2002). Analyses of correct responses included the Pc at 0-40 ms over frontal to central electrodes: F3/Z/4, FC3/Z/4, C3/Z/4 (see map 3).

Mean-amplitude values were obtained for the temporal window of each potential and submitted to repeated-measures ANOVAs. Target-related analyses consisted of one ANOVA, which tested the effects of cuing, previous congruency, electrode position and electrode side. Response-related analyses included separate ANOVAs for error and correct conditions with the factors of cuing, electrode position and electrode side. Significant effects of electrode position and electrode side were not reported, unless they involved interactions with either cuing or previous congruency. Peak latencies of the main potentials of interest (N2 and ERN) and potentials showing amplitude modulation (N1f and P3) were also subjected to ANOVAs. The latency analyses included the same temporal windows as the mean-amplitude analyses and focused on the electrode showing the highest activity: F3 electrode for the N2, N1f and ERN potentials; and Cz for the P3. The criterion to include data from a participant in either target or response-related analyses consisted of 20 artefact-free trials per condition. This criterion led to the exclusion of 2 participants from the target-related analyses and 3 participants from the response-related analyses.

Topographical analysis

The topographical analysis determined how the distribution of voltage over the scalp (topographic maps) evolved over time in each experimental condition and compared the distributions across conditions, using Cartool software (D. Brunet, Geneva, Switzerland; <https://sites.google.com/site/fbmlab/cartool>) The segmentation consisted of a spatio-temporal cluster analysis of the ERP group-averaged data normalized for global field power (with the constraints that each scalp topography should remain stable for at least 20 ms and that the correlation between different topographies should not exceed 90%). The choice of the optimal number of topographies that best explained the whole data was based on a cross-validation criterion (Pascual-Marqui, Michel, & Lehmann, 1995). The output of this segmentation analysis consists of a set of topographical maps that represent stable periods of electrical field patterns, which reflect dissociable functional states of the brain (see Figure 4, centre and bottom). Different maps reflect different stages of information processing with different underlying brain sources (Lehmann, 1987). This procedure served to guide the selection of the optimal temporal windows and electrodes for the ERP analysis. Moreover,

¹ The use of a standard keyboard as response device may have delayed (and jittered) the registration of the response event, which might explain the unusually short apparent latencies (and amplitudes) observed for the ERN.

the segmentation analysis served to compare the topographical maps and their time courses across different experimental conditions. The comparison across conditions (e.g., Figure 4, maps 2 and 3) was performed statistically at the single-subject level through a fitting procedure. The topographical maps identified for the group-average were fitted to the scalp topography of each participant and for each time point of data. During this procedure, data from each subject and condition were compared with the maps identified at the group-average level, using a spatial correlation. Each time point of the data of each participant was then labelled with the map with which it had the highest spatial correlation. For each participant, the number of milliseconds during which one specific map was present on each condition was computed. These values would indicate whether one map was dominant over another map for a given condition. These values were compared across conditions with ANOVAS with the maps and experimental conditions as factors. An interaction involving the factor map would indicate that a particular experimental condition was better explained by one map than another, and therefore that a different configuration of brain generators better explains the results.

RESULTS

Behavioural results

Error rates and mean RTs from 19 participants were submitted to separate repeated-measures ANOVAs with the factors of cuing (cued, neutral), previous congruency (congruent, incongruent) and congruency (congruent, incongruent). Error rates constituted the main dependent-variable of interest, since RTs were highly constrained by our time-pressure procedure. Table 1 shows detailed data for all conditions.

The analysis of the error rates only considered responses given within the deadline (18% rejected). The ANOVA showed a main effect of congruency (i.e., the conflict effect), $F(1,18)=80.07$, $p<.001$, so that incongruent targets induced higher error rates than congruent targets (Figure 2, top left).

A significant main effect of previous congruency, $F(1,18)=6.19$, $p=.023$, revealed that fewer errors were committed after an incongruent trial (18%) than after a congruent trial (20%). These two effects also interacted significantly leading to sequential effects² (previous congruency by congruency, $F(1,18)=8.25$, $p=.01$). Specifically, the conflict effect was smaller when the previous trial was incongruent (20%) rather than congruent (24%). Cuing also modulated the conflict effect (cuing by congruency, $F(1,18)=12.75$, $p=.002$), which was smaller on cued (19%) compared to neutral (25%) conditions. Follow-up analysis of incongruent targets showed that cuing conflict tended to reduce error rates, especially when the previous trial was congruent, $F(1,18)=3.49$, $p=.078$ (see Figure 2, bottom left).

²Given the controversy on whether sequential effects reflect top-down conflict monitoring (Kerns et al., 2004; Notebaert, Gevers, Verbruggen, & Liefoghe, 2006; Ullsperger, Bylsma, & Botvinick, 2005) or bottom-up priming effects due to stimulus-response repetitions (Mayr, Awh, & Laurey, 2003; Nieuwenhuis et al., 2006), the influence of priming was tested by including 'repetition' as a within-subjects factor (e.g., Mayr, Awh, & Laurey, 2003). Repetition exerted no influence on either the cuing by congruency interaction ($F<1$) or the previous-congruency by congruency interaction, $F(1,18)=1.27$, $p=.27$. In light of this null effect and because of restricted trial numbers, this variable was not analysed further in the ERP analyses.

The RT analysis only considered responses that were slower than 100 ms and within the deadline (14% rejected). The main effect of congruency was significant, $F(1,18)=53.1$, $p<.001$, revealing slower responses for incongruent (296 ms) compared to congruent (261 ms) trials. The main effect of cuing was also significant, $F(1,18)=26.41$, $p<.001$; responses were faster in valid versus neutral targets. The interaction between previous congruency and congruency (sequential effects) was only marginally significant, $F(1,18)=2.92$, $p=.1$, which may be due to the strong constraints placed upon speeded responses. The interaction between cuing and congruency was significant, $F(1,18)=15.1$, $p=.001$, showing larger cuing effects on congruent vs. incongruent trials (see also Gratton, Coles, & Donchin, 1992, Exp. 3). Most relevant, follow-up analysis of RTs in the incongruent condition revealed a significant effect of cuing, with faster RTs in cued (294 ms) versus neutral (299 ms) conflicting targets, $F(1,18)=5.21$, $p=.035$.

Combined, the analyses of error rates and RTs show that the anticipation of conflict can speed up and improve the performance during conflict resolution. Figure 2 (bottom) shows cuing benefits on both errors and RT to incongruent targets. The neural correlates of this attentional improvement in conflict resolution were studied by ERPs to the incongruent condition.

Electrophysiological results

Target-locked ERPs—Figure 2 (top right) shows that congruent and incongruent targets were processed differently. Consistent with previous research (Kopp, Rist, & Mattler, 1996), the frontocentral N2 was sensitive to different degrees of conflict between congruent and incongruent conditions despite being matched for stimulus frequency (50%). The conflict effect was evident as a larger and later N2 for incongruent compared to congruent targets ($F(1,16)=7.93$, $p=.01$)³. This electrophysiological correlate of conflict processing was consistent with the conflict effect observed on behaviour. Once the conflict effect was validated, the ERP analyses focused on incongruent targets yielding correct responses. These analyses tested whether processing of a conflicting stimulus was modulated by cuing when sequential effects were controlled.

The ANOVA performed on the mean amplitudes of the N2 showed an interaction between cuing and electrode side, $F(2,32)=3.57$, $p=.04$, and a further three-way interaction between cuing, previous congruency and electrode side, $F(2,32)=3.30$, $p=.05$. Together, these effects demonstrated that previous incongruent targets reliably attenuated the N2 over right frontal electrodes (F4 and FC4, $F(1,16)=4.32$, $p=.05$), but only in the absence of predictive cuing (i.e., on neutral conditions; see Figure 3 – NII vs. NCI). The N2 appeared to be attenuated by cuing over left frontal electrodes, but this did not reach statistical significance (F3 and FC3, $F(1,16)=1.37$, $p=.26$).

Crucially, the analysis of the N2 latency revealed a reliable main effect of cuing, $F(1,16)=5.15$, $p=.04$, such that the N2 peaked earlier for cued (303 ms) compared to neutral

³Note that Figure 2 shows the N2 peaking at about 250 ms for congruent targets, thus falling outside the time window used in the analysis. In any case, the conflict effect was clearly reliable for a broader time window of 240-300 ms including both incongruent and congruent N2 peaks (mean amplitude effect: $F(1,16)=11.05$, $p=.004$).

conditions (310 ms). Figure 3 (top) shows that the N2 peak and the subsequent rising occurred earlier for cued (QCI) versus neutral (NCI) conditions⁴. In contrast to cuing, previous congruency did not modulate the N2 latency ($F < 1$).

The analysis of the early N1f revealed a significant attenuation by cuing, $F(1,16)=4.42$, $p=.05$. This main effect was modulated by the congruency of the previous trial (cuing by previous congruency, $F(1,16)=4.98$, $p=.04$). When the previous trial was congruent, the N1f was clearly attenuated by the cued condition (QCI) as compared to the neutral condition (NCI), $F(1,16)=8.27$, $p=.01$ (Figure 3). When the previous trial was incongruent, the cuing effect was far from significant ($F < 1$). In contrast to cuing, previous congruency did not exert a main effect upon the N1f, $F(1,16) < 1$, in either cued (QII vs. NCI: $F(1,16)=1.66$, $p=.2$) or neutral conditions (NII vs. NCI: $F(1,16)=1.08$, $p=.3$). No significant main effects of cuing, previous congruency or interactions were observed for the latency of the N1f potential (all $F_s < 1$).

The P1 potential showed a significant interaction between cuing, previous congruency and electrode position, $F(2,32)=3.81$, $p=.03$. When effects were tested at the separate electrode locations, however, the interaction only approached a trend over electrodes PO3/4 ($F(1,16)=2.83$, $p=.11$), but remained clearly non-significant over O1/2 and PO7/8 ($p_s > .2$). The N1 analysis showed no significant effects of cuing or previous congruency ($F_s < 1$) or interactions ($p_s > .1$).

The P3 analysis also showed an interaction between cuing and previous congruency, $F(1,16)=9.20$, $p=.01$. When the previous trial was congruent, the P3 was enhanced by cued rather than neutral conditions, $F(1,16)=8.01$, $p=.01$. When the previous trial was incongruent, the cuing effect was far from significant ($F < 1$). Analogously, previous congruency was only significant on neutral conditions, $F(1,16)=7.53$, $p=.01$, rather than on cued conditions ($F < 1$). Both cuing and previous congruency effects consisted of an enhancement on the P3 amplitude. Cuing also interacted with electrode position and side, $F(6,96)=3.02$, $p=.01$, revealing the largest cuing effect over the central left electrode (C3), $F(1,16)=4.83$, $p=.04$. The latency of the P3 potential was not modulated by cuing ($F(1,16)=1.37$, $p=.26$) or previous congruency ($F < 1$).

Response-locked ERPs

Figure 4 (top) shows that errors elicited an ERN peaking shortly after the response (map 2). The ANOVA showed no effect of cuing on either ERN amplitude, $F(1,15) < 1$, or latency, $F(1,15) < 1$. The ERN was followed by two positive peaks (early and late Pe, maps 4 and 5). The ANOVAs showed no effects of cuing on the amplitudes of either early or late Pe, $F(1,15)=1.39$, $p=.26$ and $F(1,15) < 1$, respectively.

⁴It could be argued that this latency difference may have determined the mean-amplitude results. A peak-amplitude analysis was performed on the N2, which replicated the mean-amplitude data. This analysis replicated the significant interaction between cuing and electrode side ($F(2,32)=4.06$, $p=.027$), and the three-way interaction between cuing, previous congruency and electrode side, $F(2,32)=3.19$, $p=.055$, which showed that sequential effects attenuated the N2 peak amplitude over right frontal electrodes under neutral cuing conditions (mean peak amplitudes: 1.33 microvolts for previous congruent vs. 2.61 microvolts for previous incongruent; $F(1,16)=5.10$, $p=.038$).

Correct responses were associated with the correct positivity potential (Pc, map 3), which was observed in the same time range as the ERN on error conditions. The amplitude of the Pc was enhanced by cuing, $F(1,15)=14.28$, $p=.002$. Following the Pc, the topographical segmentation (Figure 4, centre) suggested that waveforms elicited by correct responses contained the same two positive potentials observed on error conditions, but greatly anticipated in time (100-150 ms earlier than in error conditions).

Topographical analysis of response-locked ERPs

Topographical analyses were performed to test the following two observations based on the morphology of the waveforms: (a) whether the ERN and Pc had different topographies associated to errors and correct responses respectively, (b) whether the similarities in the two positive peaks after the ERN and Pc for errors and correct responses, respectively, corresponded to similar topographical distributions that were offset in time.

Figure 4 (centre) shows the time course of the segmentation maps corresponding to stable voltage topographies, coloured on the global field power waveform, for each of the four conditions. The progression of maps was equivalent for all the conditions except during the time period of the ERN and Pc (maps 2 and 3). Map 2 was only present on error conditions, whereas map 3 was only present on correct responses. The topographical representation of these segments (Figure 4, bottom) showed a frontal negativity that was specific to map 2 but not map 3, which was slightly lateralised to the left hemisphere. In the group-averaged waveforms (Figure 4, top), this negativity corresponds to the ERN potential that was specifically observed on error conditions.

An ANOVA testing the preponderance of maps 2 and 3 across conditions between -100 and $+60$ ms confirmed the difference in distribution for error versus correct trials. The interaction between response and topographical map was significant, $F(1,15)=26.12$, $p<.001$. For errors, the ERN topography (map 2) was significantly dominant over map 3 (65% of the entire 160-ms temporal window vs. 35%, $t(15)=2.1$, $p=.027$, one-tailed). In contrast, for correct responses map 3 was significantly dominant over map 2, (63% vs. 37%, $t(15)=1.77$, $p=.048$, one-tailed).

The maps after the ERN map (4 to 6) followed identical sequences for both error and correct responses. The main difference consisted of map 4 (early Pe) being present for a longer duration on errors than on correct responses. This visual impression was tested by ANOVAs testing the preponderance of maps 4 and 5 for errors and correct responses over three consecutive 80-ms bins from 0 to 240 ms. The interaction between response, topographical map and time bin was significant, $F(2,30)=7.58$, $p=.002$. For errors, map 4 was significantly dominant over map 5 during the first time bin (77% vs. 23%, $t(15)=3.05$, $p=.004$, one-tailed) and the second bin (68% vs. 32%, $t(15)=2.04$, $p=.029$, one-tailed), but not at the third bin (56% vs. 44%, $t(15)=.59$, $p=.28$, one-tailed). In contrast, for correct responses map 4 was dominant over map 5 during the first time bin only (80% vs. 20%, $t(15)=3.91$, $p<.001$, one-tailed) but not at the second bin (60% vs. 40%, $t(15)=1$, $p=.18$, one-tailed). At the third bin the pattern reversed significantly, so that map 5 was now dominant over map 4 (75% vs. 25%, $t(15)=2.24$, $p=.02$, one-tailed), suggesting that the processing stage indexed by

topographical map 4 was resolved at that time for correct responses. In brief, map 4 remained for longer after errors (0-160 ms) than after correct responses (0-80 ms).

DISCUSSION

Modulation of conflict processing by proactive and reactive control

The analysis of behavioural performance confirmed that both proactive and reactive control effectively facilitated conflict resolution. This facilitation was also reflected in ERP measures. The main finding showed that proactive cuing altered the time course of conflict processing.

We expected proactive anticipation of conflict to engage increased top-down control, and hence to facilitate conflict detection, as indexed by the N2 potential. The high temporal resolution of ERPs was critical to uncover that proactive control enhanced online conflict processing by reducing the latency of the N2. This novel finding reveals the ability to prepare for conflict on the basis of predictive information. More generally, this finding confirms that top-down attention is not only constrained to cued physical attributes of forthcoming stimuli and responses (see Nobre, 2004, for a review). Rather, in the present study, cuing prompted the anticipation of conflict and the need to engage the control system for cautious stimulus-response selection. As a result, conflict was detected and resolved more rapidly. The rapid detection of conflict was particularly useful under the task parameters of the current experiment, which imposed very high temporal pressure for responding. When more deliberate processing is possible under normal conditions of time pressure (being all the remaining task parameters identical to the current experiment), the effects of proactive cuing of conflict may become less conspicuous (A. Correa, A. Rao, J. Lupiáñez, and A.C. Nobre, unpublished observations).

The temporal modulation of conflict detection by proactive control had remained unnoticed so far. Hemodynamic neuroimaging studies have provided unclear results, probably because the technique is highly insensitive to short-lived or latency effects. During the anticipatory interval, increments in ACC activation have been observed in some studies (Luks, Simpson, Feiwell, & Miller, 2002; Sohn, Albert, Jung, Carter, & Anderson, 2007) but not others (Fassbender, Foxe, & Garavan, 2006; Luks, Simpson, Dale, & Hough, 2007; MacDonald, Cohen, Stenger, & Carter, 2000). During conflict processing, decrements in ACC activation selectively related to cued conditions have been observed in some studies (Luks, Simpson, Dale, & Hough, 2007; Sohn, Albert, Jung, Carter, & Anderson, 2007) but not others (Fassbender, Foxe, & Garavan, 2006; Luks, Simpson, Feiwell, & Miller, 2002). The inconsistency of the fMRI results has then precluded establishing strong conclusions about the role of the ACC in anticipatory conflict monitoring. Importantly, however, the present ERP results strongly suggest that conflict processing can be anticipated. As recently suggested, this anticipatory mechanism may be mediated by pre-activation of the ACC during the preparatory interval (Sohn, Albert, Jung, Carter, & Anderson, 2007).

An additional explanation for the absence of proactive modulations upon ACC activity considers that the previous studies cuing conflict did not control for sequential effects. It is possible that proactive cuing could not attenuate ACC activity further when it was already

attenuated by reactive control. This possibility therefore assumes that proactive and reactive control involve common or interacting neural mechanisms. To our knowledge, the current study is the first to test this assumption by comparing neural modulation resulting from both types of control directly. The temporally rich dependent variables provided by ERPs were able to identify particular stages during which proactive and reactive control interact. From early through late neural target processing, proactive control was most effective under low reactive control. Specifically, the attenuation of the early N1f by cuing was stronger after congruent versus incongruent trials and the amplification of the late P3 was only significant after congruent trials. Analogously, reactive control was only effective in the absence of proactive control: N2 attenuation and P3 amplification by previous conflict was only significant on neutral versus cued conditions. These interactions suggest neural overlap or crosstalk between the control networks triggered by proactive and reactive signals.

The overlap between proactive and reactive control was only partial, however: each modulated conflict processing with distinct time courses and spatial distributions. The anticipatory effects of proactive control upon conflict processing started early (frontal N1 at 110 ms)⁵ and later became lateralised to the left hemisphere (P3). In contrast, the effects of reactive control started later (N2) and were lateralised to the right. Moreover, the N2 latency was selectively reduced by cuing, thus illustrating the proactive nature of this type of control over more reactive sequential effects. Overall, these findings would suggest multiple rather than a single control mechanism, although such differences could be specific to our experimental procedure. For example, signals for reactive versus proactive control took place at different times, which could have led to differential modulations of processing. Further research will be useful to clarify whether neural mechanisms subserving reactive and proactive control can be more clearly dissociated.

Our results regarding reactive control are consistent with neuroimaging research showing that increments in ACC activity on incongruent conditions correlate with subsequent reductions of ACC activity and behavioural conflict (see Botvinick, Cohen, & Carter, 2004, for a review; Durston et al., 2003), even when repetition priming effects are controlled (Kerns et al., 2004; Notebaert, Gevers, Verbruggen, & Liefoghe, 2006; see also Ullsperger, Bylsma, & Botvinick, 2005) (but see Mayr, Awh, & Laurey, 2003; Nieuwenhuis et al., 2006). Previous ERP studies controlling for priming effects have provided mixed results. In one case, the sequential modulation of conflict-related processing survived (Scerif, Worden, Davidson, Seiger, & Casey, 2006), but in another case it was abolished (Wendt, Heldmann, Munte, & Kluwe, 2007). Our behavioural analysis showed that priming did not account for the reductions in conflict effect exerted by either proactive or reactive control. Nevertheless, because we had insufficient trials to confirm our ERP results after controlling for stimulus-response repetitions, these must be taken with caution.

⁵The early N1f potential has not been specifically associated with conflict processing. However, the attentional modulation observed here is reminiscent of ERP studies on attention and emotion, which reported attenuation of the anterior N1 when fearful faces were attended (e.g., Holmes, Vuilleumier, & Eimer, 2003). Hence, it might be that our N1f was reflecting emotional processing in reaction to conflict and/or the prediction of error.

Electrophysiological correlates of error processing

Assuming that the ERN reflects ACC activity related to response-related conflict (Botvinick, Cohen, & Carter, 2004) or error detection (Debener et al., 2005), we hypothesized that the anticipation of error in conflict trials would modulate the ERN. Unexpectedly, we observed no modulation of the ERN. In light of the strong interactions between cueing and sequential effects we observed in the analysis of target-related processing, it is possible that modulation of the ERN would be detectable in conditions of low reactive control. However, to an insufficient number of error trials in the different conditions of previous congruency, this possibility could not be tested here.

The analysis of map topographies revealed that the ERN was specific to trials with incorrect responses, replicating earlier studies (Falkenstein, Hohnsbein, Hoormann, & Blanke, 1990; Gehring, Goss, Coles, Meyer, & Donchin, 1993). The absence of the typical ERN topography on 'correct' conditions replicates previous research (e.g., Ullsperger, von Cramon, & Müller, 2002), but contrasts with reports of the so-called 'correct response negativity' – CRN (Bartholow et al., 2005; Falkenstein, Hoormann, Christ, & Hohnsbein, 2000; Vidal, Hasbroucq, Grapperon, & Bonnet, 2000). The current topographical analysis showed that the ERPs associated with errors and correct responses were generated by differing configuration of neural sources, rather than differing only in the overall strength of their activation.

Rather surprisingly, the topographical analysis further revealed that, following the ERN, the stages of neural processing in error trials were equivalent to those in correct trials, though protracted in time. This finding questions the specificity of the Pe potential to error processing (Falkenstein, Hohnsbein, Hoormann, & Blanke, 1990; Falkenstein, Hoormann, Christ, & Hohnsbein, 2000). Our findings suggest instead that a common late stage of post-response processing is achieved in both correct and error trials (e.g., contextual updating), but that the conflict and/or error detection delays the onset of this stage in error trials.

In summary, proactive control based on the anticipation of conflict significantly modulated subsequent target processing, and did so through neural mechanisms that interacted with reactive control based on sequential effects. The effects of proactive control were maximal when controlled stimulus-response selection was not already engaged by reactive signals coming from conflict in the previous trial. The present findings suggest that anticipating conflict enhances cognitive control by speeding up conflict detection and resolution.

Acknowledgments

This research was supported by the Spanish Ministerio de Educación y Cultura with postdoctoral grants (EX-2005-1028 and RYC-2007-00296) to A.C. and by an award from the James S. McDonnell Foundation to A.C.N.

REFERENCES

AEEGS. American Electroencephalographic Society (AEEGS) guidelines for standard electrode position nomenclature. *Journal of Clinical Neurophysiology*. 1991; 8:200–202. [PubMed: 2050819]

- Atkinson, R.; Shiffrin, R. Human memory: A proposed system and its control processes. In: Spence, K.; Spence, J., editors. *The psychology of learning and motivation: Advances in research and theory*. Vol. Vol. 2. Academic Press; New York: 1968. p. 742-775.
- Bartholow BD, Pearson MA, Dickter CL, Sher KJ, Fabiani M, Gratton G. Strategic control and medial frontal negativity: Beyond errors and response conflict. *Psychophysiology*. 2005; 42:33–42. [PubMed: 15720579]
- Botvinick MM, Braver TS, Barch DM, Carter CS, Cohen JD. Conflict monitoring and cognitive control. *Psychological Review*. 2001; 108(3):624–652. [PubMed: 11488380]
- Botvinick MM, Cohen JD, Carter CS. Conflict monitoring and anterior cingulate cortex: an update. *Trends in Cognitive Sciences*. 2004; 8(12):539–546. [PubMed: 15556023]
- Botvinick MM, Nystrom LE, Fissell K, Carter CS, Cohen JD. Conflict monitoring versus selection-for-action in anterior cingulate cortex. *Nature*. 1999; 402(6758):179–181. [PubMed: 10647008]
- Debener S, Ullsperger M, Siegel M, Fiehler K, von Cramon DY, Engel AK. Trial-by-trial coupling of concurrent electroencephalogram and functional magnetic resonance imaging identifies the dynamics of performance monitoring. *The Journal of Neuroscience*. 2005; 25(50):11730–11737. [PubMed: 16354931]
- Durston S, Davidson MC, Thomas KM, Worden MS, Tottenham N, Martinez A, et al. Parametric manipulation of conflict and response competition using rapid mixed-trial event-related fMRI. *Neuroimage*. 2003; 20(4):2135–2141. [PubMed: 14683717]
- Eriksen BA, Eriksen CW. Effects of noise letters upon the identification of a target letter in a nonsearch task. *Perception and Psychophysics*. 1974; 16:143–149.
- Falkenstein, M.; Hohnsbein, J.; Hoormann, J.; Blanke, L. Effects of errors in choice reaction tasks on the ERP under focused and divided attention. In: Brunia, CHM.; Gaillard, AWK.; Kok, A., editors. *Psychophysiological Brain Research*. Vol. 1990. Tilburg University Press; Tilburg: 1990. p. 192-195.
- Falkenstein M, Hoormann J, Christ S, Hohnsbein J. ERP components on reaction errors and their functional significance: a tutorial. *Biological Psychology*. 2000; 51(2-3):87–107. [PubMed: 10686361]
- Fassbender C, Foxe JJ, Garavan H. Mapping the functional anatomy of task preparation: priming task-appropriate brain networks. *Human Brain Mapping*. 2006; 27(10):819–827. [PubMed: 16541457]
- Gehring WJ, Goss B, Coles MGH, Meyer DE, Donchin E. A neural system for error detection and compensation. *Psychological Science*. 1993; 4:385–390.
- Gratton G, Coles MG, Donchin E. Optimizing the use of information: strategic control of activation of responses. *Journal of Experimental Psychology: General*. 1992; 121(4):480–506. [PubMed: 1431740]
- Holmes A, Vuilleumier P, Eimer M. The processing of emotional facial expression is gated by spatial attention: evidence from event-related brain potentials. *Cognitive Brain Research*. 2003; 16(2):174–184. [PubMed: 12668225]
- Kahneman, D. *Attention and effort*. Prentice Hall; London: 1973.
- Kastner S, Ungerleider LG. Mechanisms of visual attention in the human cortex. *Annual Review of Neuroscience*. 2000; 23:315–341.
- Kerns JG, Cohen JD, MacDonald AW III, Cho RY, Stenger VA, Carter CS. Anterior cingulate conflict monitoring and adjustments in control. *Science*. 2004; 303:1023–1026. [PubMed: 14963333]
- Kopp B, Rist F, Mattler U. N200 in the flanker task as a neurobehavioral tool for investigating executive control. *Psychophysiology*. 1996; 33:282–294. [PubMed: 8936397]
- Lehmann, D. Principles of spatial analyses. In: Gevins, AS.; Remond, A., editors. *Handbook of electroencephalography and clinical neurophysiology: Methods of analysis of brain electrical and magnetic signals*. Vol. Vol. 1. Elsevier; Amsterdam: 1987. p. 309-354.
- Logan GD, Zbrodoff NJ. Constraints on strategy construction in a speeded discrimination task. *Journal of Experimental Psychology: Human Perception and Performance*. 1982; 8:502–520. [PubMed: 6214604]
- Luks TL, Simpson GV, Dale CL, Hough MG. Preparatory allocation of attention and adjustments in conflict processing. *Neuroimage*. 2007; 35(2):949–958. [PubMed: 17258912]

- Luks TL, Simpson GV, Feiwell RJ, Miller WL. Evidence for anterior cingulate cortex involvement in monitoring preparatory attentional set. *Neuroimage*. 2002; 17(2):792–802. [PubMed: 12377154]
- MacDonald AW, Cohen JD, Stenger VA, Carter CS. Dissociating the role of the dorsolateral prefrontal and anterior cingulate cortex in cognitive control. *Science*. 2000; 288:1835–1838. [PubMed: 10846167]
- Mayr U, Awh E, Laurey P. Conflict adaptation effects in the absence of executive control. *Nature Neuroscience*. 2003; 6:450–452.
- Monsell S. Task switching. *Trends in Cognitive Sciences*. 2003; 7(3):134–140. [PubMed: 12639695]
- Müller HJ, Rabbitt PM. Reflexive and voluntary orienting of visual attention: time course of activation and resistance to interruption. *Journal of Experimental Psychology: Human Perception and Performance*. 1989; 15(2):315–330. [PubMed: 2525601]
- Nieuwenhuis S, Stins JF, Posthuma D, Polderman TJ, Boomsma DI, de Geus EJ. Accounting for sequential trial effects in the flanker task: conflict adaptation or associative priming? *Memory and Cognition*. 2006; 34(6):1260–1272. [PubMed: 17225507]
- Nobre, AC. Probing the flexibility of attentional orienting in the human brain. In: Posner, MI., editor. *Cognitive Neuroscience of Attention*. Guilford Press; New York: 2004. p. 157-179.
- Norman, DA.; Shallice, T. Attention to action: Willed and automatic control of behaviour. In: Davidson, RJ.; Schwartz, GE.; Shapiro, D., editors. *Consciousness and Self-Regulation: Advances in Research and Theory*. Plenum Press; New York: 1986. p. 1-18.
- Notebaert W, Gevers W, Verbruggen F, Liefvooghe B. Top-down and bottom-up sequential modulations of congruency effects. *Psychonomic Bulletin and Review*. 2006; 13(1):112–117. [PubMed: 16724777]
- Pascual-Marqui RD, Michel CM, Lehmann D. Segmentation of brain electrical activity into microstates: Model estimation and validation. *IEEE Transactions on Biomedical Engineering*. 1995; 42:658–665. [PubMed: 7622149]
- Rabbitt PMA. Errors and error correction in choice reaction tasks. *Journal of Experimental Psychology*. 1966; 71:264–272. [PubMed: 5948188]
- Ridderinkhof KR, Ullsperger M, Crone EA, Nieuwenhuis S. The role of the medial frontal cortex in cognitive control. *Science*. 2004; 306(5695):443–447. [PubMed: 15486290]
- Scerif G, Worden MS, Davidson M, Seiger L, Casey BJ. Context modulates early stimulus processing when resolving stimulus-response conflict. *Journal of Cognitive Neuroscience*. 2006; 18:781–792. [PubMed: 16768377]
- Sohn MH, Albert MV, Jung K, Carter CS, Anderson JR. Anticipation of conflict monitoring in the anterior cingulate cortex and the prefrontal cortex. *Proceedings of the National Academy of Sciences of the United States of America*. 2007; 104(25):10330–10334. [PubMed: 17563353]
- Stroop JR. Studies of interference in serial verbal reactions. *Journal of Experimental Psychology*. 1935; 18:643–662.
- Ullsperger M, Bylsma LM, Botvinick MM. The conflict adaptation effect: it's not just priming. *Cognitive, Affective and Behavioral Neuroscience*. 2005; 5(4):467–472.
- Ullsperger M, von Cramon DY, Müller NG. Interactions of focal cortical lesions with error processing: evidence from event-related brain potentials. *Neuropsychology*. 2002; 16(4):548–561. [PubMed: 12382993]
- van Veen V, Carter CS. The timing of action-monitoring processes in the anterior cingulate cortex. *Journal of Cognitive Neuroscience*. 2002; 14(4):593–602. [PubMed: 12126500]
- Vidal F, Hasbroucq T, Grapperon J, Bonnet M. Is the 'error negativity' specific to errors? *Biological Psychology*. 2000; 51(2-3):109–128. [PubMed: 10686362]
- Wendt M, Heldmann M, Munte TF, Kluwe RH. Disentangling Sequential Effects of Stimulus- and Response-related Conflict and Stimulus-Response Repetition using Brain Potentials. *Journal of Cognitive Neuroscience*. 2007; 19(7):1104–1112. [PubMed: 17583987]

Figure 1.

The main events of the task. The four conditions included in the stimulus-locked analysis are displayed. This analysis included current incongruent targets with the factors of cuing (cued, neutral) and previous congruency (congruent, incongruent). QCI: cued, previous congruent, current incongruent target; QII: cued, previous incongruent, incongruent; NCI: neutral, previous congruent, incongruent; NII: neutral, previous incongruent, incongruent.

Figure 2.

Top: Behavioural (left) and electrophysiological (right) correlates of the conflict effect.

Target-locked ERP waveforms averaged across 17 participants for congruent and incongruent trials. The frontal N2 potential was larger and peaked later for incongruent vs. congruent conditions. **Bottom:** Mean error rates (left) and RTs (right) from the incongruent condition as a function of cuing (cued, neutral) and previous congruency (congruent, incongruent). Vertical bars represent standard errors.

Figure 3.

Top: Stimulus-locked ERP waveforms averaged across 17 participants showing the effects of cueing (top row) and sequential effects (bottom row) over the frontal electrode sites (F3 (left), Fz (midline) and F4 (right)) where the N2 potential was largest. To illustrate the proactive, cueing effects, waveforms elicited by *cued* incongruent targets preceded by congruent targets (QCI, thick blue line) are compared with neutral incongruent targets preceded by congruent targets (NCI, thin black line). To illustrate the reactive, sequential effects, waveforms elicited by neutral incongruent targets preceded by incongruent targets (NII, thick purple line) are compared with neutral incongruent targets preceded by congruent targets (NCI, thin black line). The significant effects on the N1f and N2 potentials are labelled where they were strongest. The P3 effects occurred more posteriorly, and are not shown in the figure. **Bottom:** Topographical representation of the voltage distribution over the scalp averaged during each segmentation map. Positive voltage is plotted in red, and negative voltage is plotted in blue. Voltage was normalised during each time period shown, according to the scale provided on the right. Yellow dots show the electrode montage.

Figure 4.

Top: Response-locked ERP waveforms averaged across 16 participants for errors (red) and correct responses (green) as a function of cuing (cued – solid line, neutral – dashed line). ERPs recorded at frontocentral electrodes are shown (left, centre and right electrode sides are collapsed in this figure). The main error-related potentials are labelled (ERN: error-related negativity; PEe/PEI: early/late error positivity). On errors, the ERN and PE did not differ for cued versus neutral conditions. On correct responses, the first positive potential was enhanced by cuing. **Centre:** Segmentation maps of the group-averaged data for the four conditions during the interval between -600 and +700 ms (zero indicates response execution - key pressing). Map 2 was present on errors, whereas map 3 was present on correct responses. Maps 4, 5 and 6 followed the same sequence for both errors and correct responses. Map 4 was longer after errors compared to correct responses. **Bottom:** Topographical representation of the voltage distribution over the scalp averaged across each segmentation map. Map 2 shows the ERN distribution as a negative voltage (blue) over the frontal part of the head.

Table 1

Mean RTs and error rates from 19 participants broken down by cuing (cued, neutral), previous congruency (congruent, incongruent) and congruency (congruent, incongruent). Standard errors are shown in brackets.

Cued				Neutral			
Previous Congruent		Previous Incongruent		Previous Congruent		Previous Incongruent	
Congruent	Incongruent	Congruent	Incongruent	Congruent	Incongruent	Congruent	Incongruent
252 (6.8)	295 (10.5)	253 (6.8)	293 (9.4)	267 (7.6)	300 (11.8)	271 (8.2)	298 (11)
11 (1.8)	30 (2.5)	10 (1.7)	27 (2.8)	6 (1.1)	34 (2.4)	6 (1.1)	28 (2.5)