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Conflict monitoring and error processing: New insights from simultaneous EEG–fMRI

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ABSTRACT

Error processing and conflict monitoring are essential executive functions for goal directed actions and adaptation to conflicting information. Although medial frontal regions such as the anterior cingulate cortex (ACC) and the pre-supplementary motor area (pre-SMA) are known to be involved in these functions, there is still considerable heterogeneity regarding their spatio-temporal activations. The timing of these functions has been associated with two separable event-related potentials (ERPs) usually localized to the medial frontal wall, one during error processing (ERN — error related negativity) and one during conflict monitoring (N2).

In this study we aimed to spatially and temporally dissociate conflict and error processing using simultaneously recorded EEG and fMRI data from a modified Flanker task in healthy adults. We demonstrate a spatial dissociation of conflict monitoring and error processing along the medial frontal wall, with selective conflict level dependent activation of the SMA/pre-SMA. Activation to error processing was located in the ACC, rostral cingulate zone (RCZ) and pre-SMA. The EEG-informed fMRI analysis revealed that stronger ERN amplitudes are associated with increased activation in a large coherent cluster comprising the ACC, RCZ and pre-SMA, while N2 amplitudes increased with activation in the pre-SMA. Conjunction analysis of EEG-informed fMRI revealed common activation of ERN and N2 in the pre-SMA and divergent activation in the RCZ. No conjoint activation between error processing and conflict monitoring was found with standard fMRI analysis along the medial frontal wall.

Our fMRI findings clearly demonstrate that conflict monitoring and error processing are spatially dissociable along the medial frontal wall. Moreover, the overlap of ERN- and N2-informed fMRI activation in the pre-SMA provides new evidence that these ERP components share conflict related processing functions and are thus not completely separable.

1. Introduction

Goal directed behavior requires the suppression of inappropriate responses under conflicting information. Conflict may thereby occur at different levels of information processing (van Veen et al., 2001) such as stimulus encoding, response selection, response execution and response evaluation. One of the most frequently used experimental paradigms to study conflict processing is the Eriksen Flanker task (Eriksen and Eriksen, 1974), which requires a speeded response to target stimuli flanked by either congruent or incongruent peripheral distractor stimuli.

A large body of neuroimaging methods examined conflict monitoring and error processing to elucidate the underlying involvement of brain networks. Some studies tried to disentangle the role of specific parts of the medial frontal cortex during different levels and aspects of conflict processing such as conflict detection, monitoring and evaluation of the outcome of actions. The pre-supplementary motor area (pre-SMA) thereby might be especially important in resolving response conflict between incompatible, competing motor plans by triggering response switching before an overt response is given (Garavan et al., 2003; Hazeltine et al., 2000; Nachev et al., 2005; Ullsperger and von Cramon, 2001; Zysset

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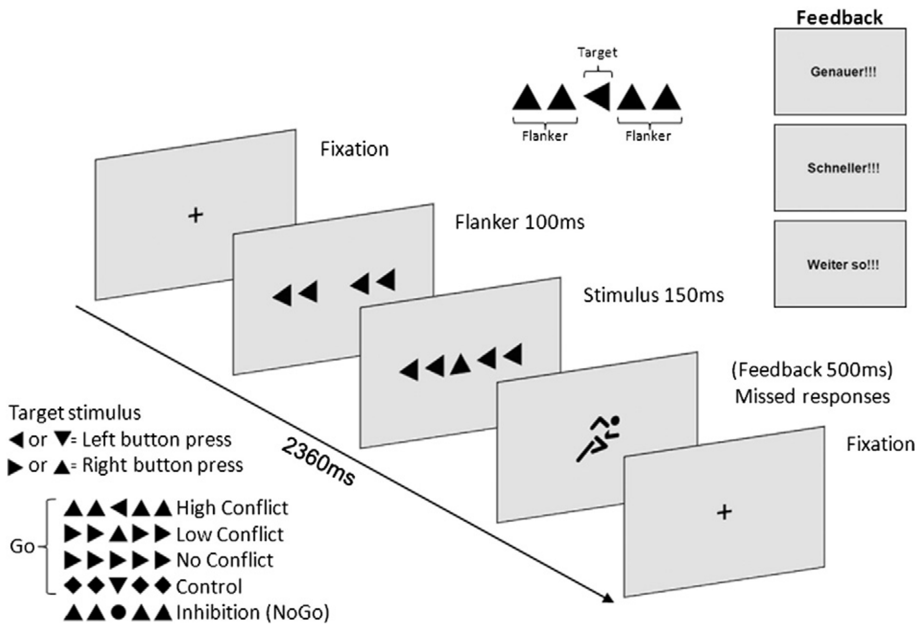

Fig. 1. Trial timing and conditions of the modified novel flanker task (for details, see main text).

et al., 2001). On the other hand, the rostral cingulate zone (RCZ) – corresponding to the rostral cingulate motor area (CMAr) in primates (cf. Picard and Strick (2001)) – showed enhanced activation during error processing (Braver et al., 2001; Garavan et al., 2003; Kiehl et al., 2000; Nee et al., 2011; Ullsperger and von Cramon, 2001) (for review of conflict and error findings see also (Ridderinkhof et al., 2004)). Braver and colleagues (2001) discussed the possibility of a continuous functional differentiation along the caudal–rostral and superior–inferior dimensions of the ACC. Accordingly, more superior caudal regions show enhanced responsiveness to conflict on the selection and execution level while rostral and inferior regions are more sensitive to processing errors and related affective components.

The N2 or N200 is a strong (fronto-)central negative deflection peaking at around 200–300 ms after stimulus onset, is associated with conflict monitoring (Donkers and van Boxtel, 2004; Enriquez-Geppert et al., 2010; Larson et al., 2014; Randall and Smith, 2011; Yeung et al., 2004) and is especially pronounced in tasks inducing high conflict situations such as in Flanker tasks. A similar topography as the N2 can be found for the error-related negativity (ERN/Ne), a response locked ERP occurring after the commission of errors. Its strong negative frontocentral deflection peaks 50–120 ms after erroneous responses (Falkenstein et al., 1990; Gehring et al., 1993). Not only errors but also correct responses (correct response negativity (CRN)) (Falkenstein et al., 2000) or feedbacks (feedback related negativity (FRN)) (Holroyd and Coles, 2002; Miltner et al., 1997) may evoke components with ERN-like topographies. Similar to the anatomical origin of the FRN peaking 200–300 ms after feedback onset (Hauser et al., 2014a; Hauser et al., 2014b) (for review see Ullsperger et al. (2014)), the sources of the ERN are also supposed to lie in the ACC: EEG–fMRI and source localization studies localized the ERN activity to the ACC of the frontomedial wall (Debener et al., 2005; Holroyd et al., 1998; Van Veen and Carter, 2002b). Some source localization studies also suggest that the ERN and the N2 share conflict monitoring processes and a common neural substrate despite their temporally distinct appearance in the processing of information either prior to correct responses or after erroneous responses (Van Veen and Carter, 2002b; Yeung et al., 2004). Conflict monitoring processes are thus assumed to modulate ERPs at multiple levels during stimulus (N2) and response level (ERN, CRN) processing (Olvet and Hajcak, 2008).

While fMRI offers a high spatial resolution that allows accurate localization and delineation of the hemodynamic correlates of neuronal activation, it has rather poor temporal resolution due to the relatively slow BOLD (blood oxygenation-level-dependent) response. The event-related potentials (ERPs) of the EEG, on the other hand, provide precise insights into the timing of these executive processes, although with rather limited spatial resolution. The simultaneous application of EEG and fMRI, as in the present study, takes advantage of both techniques. In the EEG-informed fMRI analysis approach (Debener et al., 2006), the coupling between the hemodynamic and electrical signals has been explored. Only few studies have investigated error processing and conflict monitoring using single trial analyses. One of them is the study by Debener et al. (2005) who reported that the BOLD signal correlated with independent component based single trial amplitudes of the ERN in the RCZ. In a recent study of Baumeister et al. (2014), response inhibition and attention allocation – represented by the N2/P3 of the event-related potential (ERP) – were investigated by capturing the spontaneous trial-by-trial variation of the corresponding BOLD signal. Higher N2 amplitudes were associated with deactivations in specific parts of the default mode network (DMN), such as the precuneus, superior temporal gyrus and medial frontal gyrus. Another multimodal study correlated the N2/P3 single trial ERP amplitudes with independent component activity from fMRI data and revealed that the pre-SMA was activated during both stop and error trials while it was not responsive to conflict (Huster et al., 2011). These findings suggest the pre-SMA to be involved in inhibitory mechanisms rather than conflict processing per se.

Despite the hypothesis from previous studies for spatially dissociable error and conflict monitoring processes in the ACC and pre-SMA (Garavan et al., 2003; Nee et al., 2011) and for shared conflict monitoring functions of the N2 and ERN (Olvet and Hajcak, 2008), direct evidence confirming this hypothesis is still lacking. In the present study we used simultaneous EEG–fMRI to spatially and temporally dissociate conflict monitoring and error processing by using a modified Flanker task that includes a manipulation of conflict level to induce errors. In a first step, we examined the fMRI-based spatial overlap and dissociation of error and conflict processing along the medial frontal wall (Garavan et al., 2003; Nee et al., 2011) by whole brain and region of interest analyses along the frontal medial wall. Secondly, we applied trial-by-trial