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Errors can be related to pre-stimulus differences in ERP topography and their concomitant sources

Juliane Britz [a,b,c,*], Christoph M. Michel [a,b,c,d]

[a] Department of Fundamental Neuroscience, Centre Médical Universitaire, University of Geneva, 1, Rue Michel Servet, CH-1211 Geneva, Switzerland
[b] Geneva Neuroscience Center, University of Geneva, Geneva, Switzerland
[c] EEG Brain Mapping Core, Center for Biomedical Imaging of Lausanne & Geneva (CIBM), Geneva, Switzerland
[d] Department of Neurology, University Hospital, Geneva, Switzerland

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ABSTRACT

Much of the variation in both neuronal and behavioral responses to stimuli can be explained by pre-stimulus fluctuations in brain activity. We hypothesized that also errors are the result of stochastic fluctuations in pre-stimulus activity and investigated the temporal dynamics of the scalp topography and their concomitant intracranial generators of stimulus- and response-locked high-density event-related potentials (ERPs) to errors and correct trials in a Stroop task. We found significant differences in ERP map topography and intracranial sources before the onset of the stimulus and after the initiation of the response but not as a function of stimulus-induced conflict. Before the stimulus, topographic differences were accompanied by differential activity in lateral frontal, parietal and temporal areas known to be involved in voluntary reorientation of attention and cognitive control. Differential post-response activity propagated both medially and laterally on a rostral–caudal axis of a network typically involved in performance monitoring. Analysis of the statistical properties of error occurrences revealed their stochasticity.

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Introduction

Much of the variance of both neuronal and behavioral responses to stimuli can vary largely as a function of the pre-stimulus state of the brain. This pertains to spatial scales from single cells embedded in their local population to ERP map topographies and can be observed both in terms of longer-lasting aspects of pre-stimulus activity as well as the activity at the very moment of stimulus arrival. Pre-stimulus differences can affect both quantitative aspects of stimulus processing such as differences in reaction times and qualitative aspects such as detection or interpretation of stimuli. On the cellular level, variations in the magnitude of evoked responses have been related to both pre-stimulus fluctuations in membrane potentials (Azouz and Gray, 1999) and the overall state of the network a single neuron is embedded in (Arieli et al., 1996). On a global level, the ERP topography elicited by physically identical stimuli has been found to vary as a direct function of the immediate pre-stimulus topography (Kondakor et al., 1997; Kondakor et al., 1995; Lehmann et al., 1994). Quantitative behavioral aspects of stimulus processing, i.e. faster reaction times have been related to pre-stimulus power in the EEG gamma band both in monkeys (Womelsdorf et al., 2006) and humans (Gonzalez Andino et al., 2005). Likewise, slower reaction times have been consistently related to increased alpha power (Hanslmayr et al., 2007; Kranczioch et al., 2007; Romei et al., 2008a; Thut et al., 2006). Qualitative behavioral aspects of stimulus processing such as e.g. target detection and phosphene perception could be similarly related to pre-stimulus differences in alpha phase (Busch et al., 2009) and power (Hanslmayr et al., 2005; Rihs et al., 2007; Rihs et al., 2009; Thut et al., 2006; Romei et al., 2008a; Romei et al., 2008b). Other qualitative differences such as hemispheric lateralization in language processing (Mohr et al., 2005) or the perceptual interpretation of a bi-stable stimulus (Britz et al., 2009) could be related to the momentary state of the brain at stimulus onset as indexed by the EEG map topography. Thus, physically identical stimuli can undergo mutually exclusive fates as a function of momentary intrinsic brain dynamics before stimulus onset.

In the present study we took this assumption one step further and investigated whether error commission could also be attributed to differences in brain state in the time window immediately before stimulus arrival rather than to stimulus properties per se. Errors occur randomly, i.e. without a regular periodicity, and irrespective of physical stimulus properties. Errors are of course committed more likely under conditions of conflict or interference, i.e. when different response alternatives are mapped onto the same stimulus. It is important to note however, that errors are also committed in the absence of conflict or interference. Accordingly, differences before stimuli that are subsequently responded to correctly or erroneously should be the same irrespective of whether that stimulus induces a

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* Corresponding author. Department of Fundamental Neuroscience, Centre Médical Universitaire, University of Geneva, 1, Rue Michel Servet, CH-1211 Geneva, Switzerland. Fax: +41 22 379 5728.
E-mail address: juliane.britz@unige.ch (J. Britz).

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conflict or not. We hypothesized that pre-stimulus differences can lead to error commission rather than stimulus-induced conflict. Whether errors are committed because of failure in cognitive control or an incorrect stimulus–response mapping cannot be answered with the task used here.

We used a Stroop task because the mapping of multiple response alternatives onto the same stimulus induces conflict, which increases the likelihood of error commission. This enabled us to disentangle pre-stimulus and post-stimulus effects on errors. Effects of error commission as a consequence of pre-stimulus differences should manifest irrespective of conflict before stimulus onset. Error commission as a consequence of conflict should manifest after stimulus onset as a function of stimulus-induced conflict. We modified the Stroop task such that each response (i.e. each color) was mapped onto one finger. This was done to avoid contamination of the EEG by articulation-related muscle artifacts and to have distinct behavioral measures for each response alternative and clearly identifiable events for the computation of response-locked ERPs. We are aware that this induced a complex stimulus–response mapping which had to be held in working memory; note however, that this additional taxing on working memory affected both the conflict and non-conflict trials equally.

The consequences of error commission have been widely investigated. Errors elicit a large centrally distributed negativity (error-related negativity, ERN) which peaks at around 100 ms after response execution and whose generator has been localized in the anterior cingulate cortex (ACC) (Carter et al., 1998; Carter and van Veen, 2007; Debener et al., 2005; van Veen and Carter, 2002b). More recently, transient synchronous activity in the EEG theta band has been identified as the most likely generator of the ERN (Cavanagh et al., 2009; Luu et al., 2004; Trujillo and Allen, 2007). Theta power, i.e. coherent phase locking in the theta frequency band, has been found to decrease in trials preceding errors and to increase immediately after the commission of an error.

The erroneously treated stimuli themselves on the other hand have received surprisingly little attention and are usually discarded as − errors. Previous studies have found larger positive deflections (error-preceding positivity, EPP) at two central electrodes in the first 100 ms after the response in trials preceding an error than a correct response (Hajcak et al., 2005; Ridderinkhof et al., 2003). This has been interpreted as fluctuations in the efficiency of action monitoring without further investigations of concomitant sources. If errors are indeed foreshadowed by decreased levels of action monitoring, these differences should manifest beyond the first 100 ms after response execution. If such transient failures of action monitoring are the cause for errors in a subsequent trial, they should manifest in time-locked differences in action monitoring and cognitive control, and this should still be observed immediately before stimulus onset in a subsequent trial.

We hypothesized that errors can be related to stochastic fluctuations in pre-stimulus differences in brain state and disentangled the time course of both stimulus- and response-locked brain activity in a Stroop task (MacLeod, 1991) by means of Electrical Neuroimaging (Michel et al., 2004; Murray et al., 2008). We investigated differences in ERP scalp topographies as a function of error commission. Since different topographies have necessarily different intracranial generators, we also estimated differences in their concomitant sources. Like all EEG/MEG source localization methods, the distributed inverse solutions are non-unique and depend on the implemented constraints and the regularization parameters. However, numerous experimental and clinical studies have shown that the constraints introduced in the distributed linear inverse solutions lead to reasonable results. Such studies included direct comparison with intracranial recordings and electrocortical stimulation (Fuchs et al., 1999; Lantz et al., 1996; Michel et al., 1999a; Zumsteg et al., 2006), with fMRI (Groening et al., 2009; Schulz et al., 2008; Vulliemoz et al., 2009) and with post-surgical outcome (Michel et al., 2004; Sperli et al., 2006).

In the framework of the current hypothesis, namely that errors are the consequence of pre-stimulus differences in brain activity rather than the mere presence of conflict, the distinction between errors and correct responses should manifest before the onset of the stimulus and after the initiation of the response irrespective of the stimulus-induced conflict.

Methods

Subjects

Eleven subjects (five female) participated in exchange for monetary compensation. All were right-handed (Oldfield, 1971), native speakers of French and had normal or corrected-to-normal visual acuity and none had any current or prior neurological or psychiatric impairments. Mean age of participants was 27.63 years (range 20–31 years). Prior to participation, subjects provided written informed consent that had been approved by the Medical Ethics Committee of the University Hospital of Geneva in compliance with the Declaration of Helsinki.

Stimuli and procedure

Stimuli were four French color words for red, yellow, green and blue (“rouge”, “jaune” , “vert”, “bleu”) each written in red, blue, green and yellow, respectively. In congruent trials, the ink color and the color word referred to the same, and in incongruent trials they referred to different colors. Stimuli were presented in the center of a CRT screen for 200 ms and subtended ~2.5° of horizontal visual angle. Subjects were seated about 100 cm from the screen and were instructed to indicate the color of the ink by using their right hand (index = red, middle = yellow, ring = green, pinkie = blue). This was done to avoid contamination of the EEG by muscular artifacts associated with the pronunciation of the color. Prior to the EEG experiment, a behavioral training session familiarized subjects with the procedure and allowed them to practice the association of the ink colors with the corresponding fingers.

Each trial started with the presentation of a fixation cross whose duration was randomly varied between 500 and 2000 ms; this was done to prevent subjects from anticipating the precise onset of the stimulus presentation. The stimulus was presented for 200 ms followed by a fixation cross which remained on the screen until the response (max. 2000 ms). After the response, a feedback was given to the subjects (200 ms), then the fixation cross reappeared for 500 ms and it turned green for 1000 ms to indicate the time period when subjects were allowed to blink (see Fig. 1). Subjects were instructed to

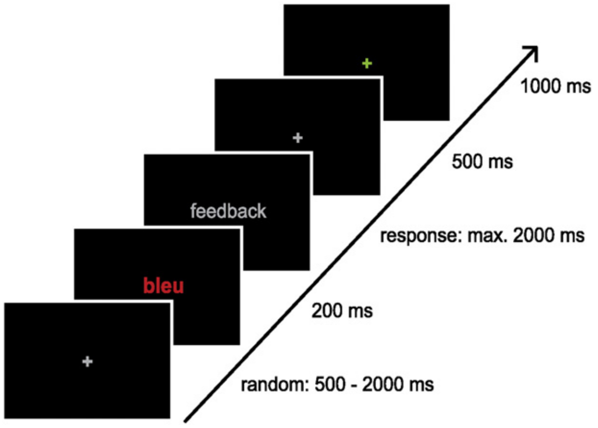

Fig. 1. Experimental procedure. After a random inter-trial interval, the stimulus was displayed for 200 ms, and response feedback was given. The green cross indicated when subjects were allowed to blink.

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