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Wronger than wrong: Graded mapping of the errors of an avatar in the performance monitoring system of the onlooker

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ABSTRACT

EEG studies show that observing errors in one's own or others' actions triggers specific electro-cortical signatures in the onlooker's brain, but whether the brain error-monitoring system operates according to graded or discrete rules is still largely unknown. To explore this issue, we combined immersive virtual reality with EEG recording in participants who observed an avatar reaching-to-grasp a glass from a first-person perspective. The avatar could perform correct or erroneous actions. Erroneous grasps were defined as small or large depending on the magnitude of the trajectory deviation from the to-be-grasped glass. Results show that electro-cortical indices of error detection (indexed by ERN and mid-frontal theta oscillations), but not those of error awareness (indexed by error-Positivity), were gradually modulated by the magnitude of the observed errors. Moreover, the phase connectivity analysis revealed that enhancement of mid-frontal theta phase synchronization paralleled the magnitude of the observed error. Thus, theta oscillations represent an electro-cortical index of the degree of control exerted by mid-frontal regions whose activation depends on how much an observed action outcome results maladaptive for the onlooker. Our study provides novel neurophysiological evidence that the error monitoring system maps observed errors of different magnitude according to fine-grain, graded rather than all-or-none rules.

Introduction

Detecting and monitoring errors in one's own and others' actions is crucial for the optimal adaptation of goal-directed behaviours, as well as for social interactions. Studies demonstrate the existence of specific EEG signatures associated with the detection of errors committed by the self or observed in others (Ullsperger et al., 2014a). More specifically, two main event-related potentials (ERPs) are inherently linked to error monitoring, namely i) Error-Related Negativity (ERN), a negative deflection peaking over frontocentral electrodes (Gehring et al., 1993; Taylor et al., 2007), and ii) error positivity (Pe), a more sustained positive-going component (Falkenstein et al., 2000). The Pe can be further classified into an earlier frontocentral Pe (early Pe) following the ERN, and a centroparietal Pe (late Pe). The ERN and the Pes are associated with different neurocognitive functions in the complex architecture of the performance monitoring system. Indeed, while the ERN may underlie conflict monitoring (Botvinick et al., 2001; Yeung et al., 2004), feedback-based learning (Holroyd and Coles, 2002), or action outcome predictions (Quilodran et al., 2008; Alexander and Brown, 2011), the early and late- Pe may predominantly reflect a stimulus-driven reorienting response after errors and error awareness respectively (Endrass et al., 2007; Ridderinkhof et al., 2009; Steinhauser and Yeung, 2010; Wessel et al., 2012; Ullsperger et al., 2014b; Boldt and Yeung, 2015; Di Gregorio et al., 2016). In addition to the error-related ERPs, analysis of oscillatory brain activity indicates that an increase of mid-frontal theta power (4–8 Hz) may also play a crucial role in the error detection process (Luu et al., 2000; Trujillo and Allen, 2007; Cavanagh et al., 2012; Cavanagh and Shackman, 2015). Studies suggest, for example, that mid-frontal theta oscillations may be the vehicle by which mid- and lateral-frontal brain regions (Cohen, 2014) interact in order to process negative outcomes and eventually call for appropriate top-down cognitive control (Brázdil et al., 2009; Cavanagh et al., 2009). Crucially, mid-frontal theta oscillations and ERN are functionally linked and seem to originate from the same cortical regions (Van Veen and Carter, 2001;

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Cohen et al., 2008; van Noordt et al., 2017).

Relevant to the present study is that both ERN and Pe are elicited (with delayed latencies) when people observe errors. They are thus referred to as observation-ERN (oERN) and observation-Pe (oPe; van Schie et al., 2004; Bates et al., 2005; Koban et al., 2010; de Bruijn and von Rhein, 2012). Also, our previous EEG and virtual reality study (Pavone et al., 2016) shows that mid-frontal theta oscillations can be elicited when people observe erroneous actions in first-person perspective (1PP). Although early studies on error observation (van Schie et al., 2004) suggest that seeing errors in others' actions provides an onlooker's motor system with appropriate cues as to how to implement flexible environmental interactions, very little is known about how such a process is actually implemented at a cortical level, or whether it is marked by specific neurophysiological signatures. However, understanding how the error monitoring system is sensitive to the magnitude of an error - be it observed or executed - is fundamental for comprehending the very nature of the performance monitoring systems in ecological conditions. Importantly, while goal-directed behaviours entail continuous performance monitoring, the neural signatures of action monitoring have predominantly been studied in speeded-response tasks where errors are all-or-none. Crucially, however, given the variety of errors that people experience in daily life, all-or-none paradigms may not capture the ecological essence of error monitoring or the brain responses elicited by different types of errors. Interestingly, the seminal study by Gehring et al. (1993) showed how different parameters of compensatory behaviour after error commission were directly modulated by the amplitude of the ERN. Moreover, further studies acknowledged the importance of graded errors by: i) disrupting the control of a joystick during tracking tasks (Anguera et al., 2009; de Bruijn et al., 2003; Krigolson and Holroyd, 2006; Krigolson et al., 2008), ii) manipulating the usability of stimuli with masking-procedures (Maier et al., 2008), iii) using prismatic goggles to induce visual-motor mismatch (Vocat et al., 2011), iv) using force-inducing robotic devices to disturb participants' responses (Torrecillos et al., 2014, 2015), or v) studying the gradual or sudden trajectory mismatch of a cursor (Omedes et al., 2015). Also, recent EEG investigations provided conflicting findings on whether the processing of graded negative feedbacks modulates brain responses in a binary (Spüler and Niethammer, 2015; Janssen et al., 2016) or parametrical way (Luft et al., 2014). It is still largely unknown, therefore, whether the performance monitoring system maps action errors in a graded or discrete way.

To address this question, here we combined EEG and immersive virtual reality in an innovative set-up to investigate whether the magnitude of observed action errors induces graded modulation of the performance monitoring system and of its electro-cortical and behavioural signatures.

Materials and methods

Participants

Twenty-four right-handed participants (12 females; mean age ± SD: 24.6 ± 2.9 years) took part in the study. They had normal or corrected-to-normal visual acuity and reported no history of neurological/psychiatric diseases. The experimental protocol was approved by the Santa Lucia Foundation Ethics Committee and conducted in accordance with the ethical standards of the 2013 Declaration of Helsinki. Data from two subjects were discarded because EEG artifacts were present in more than 25% of trials. Thus, all analyses were performed on 22 subjects (10 females; mean age ± SD: 24.4 ± 3.1 years).

Apparatus and stimuli

Participants were seated in a four-screens immersive virtual environments (i.e., CAVE system; Cruz-Neira et al., 1992, Fig. 1 panel A). The virtual scenario consisted in a room (5 × 5 × 3 m) with a virtual table (1.2 × 0.8 × 0.8 m). Atop the virtual table was a green parallelepipedon with a blue glass placed on it. An avatar sat with the right upper-limb resting on the virtual table at ~50 cm from the glass (Fig. 1 panel B). The avatar and the scenario were digitally drawn on a 1:1 scale by Autodesk Maya 2011 and Autodesk 3Ds Max 2011 respectively, and implemented in XVR 2.1 (http://www.vrmedia.it/en.html; Tecchia et al., 2010). The avatar's kinematics was rendered in XVR using Halca libraries (Gillies and Spanlang, 2010). The 3D images were alternatively eye-by-eye displayed by Nvidia Stereo Glasses (refresh rate: 60 Hz). These were interfaced with an Intersense 900 ultrasonic system (Thales Visionix; 6 degrees of freedom) that allowed participants' head movements to be tracked in real-time. Both the CAVE system and XVR were interfaced with the EEG amplifier by a TriggerStation TS832U (Braintrends ltd; http://www.braintrends.it) that allowed to control marker events with nanosecond precision.

Procedure

The paradigm consisted in the 1PP observation of simple reach to grasp a glass actions performed by a virtual actor, and was split in two tasks. In the first experiment (EEG task), continuous EEG was recorded while participants underwent passive action observation, whereas the second experiment (RTs task) consisted in a speeded-response task (without EEG recording), in which participants were asked to press a key on a response-pad as soon as they detected an error in the observed avatar's action. The RTs task served to i) acquire behavioural index of the time taken by the onlooker to detect observed errors and ii) to control for possible discrepancy in the detection of errors of different sizes (see Supplementary Materials for more details).

The EEG task was preceded by a calibration procedure in which each participant was placed into the CAVE system. Then, participants' body was occluded by a cloth and aligned with the virtual body, resulting in the so-called 1PP. This allowed us to perfectly match participants' viewing point with the viewing point of the virtual actor who was going to perform the actions to observe. Tellingly, the CAVE system allowed us to combine experimental control with ecology during action observation, and provided participants with a high level of immersivity in the virtual environment.

Before the EEG task started, participants were required to keep their own right upper-limb extended along their right side for the whole duration of the experiment.

Fig. 1 panel C depicts the time-line of the paradigm. Each trial started with the virtual right arm resting on the table. After a synthesized voice instructed the avatar to grasp the glass (2000 ms), participants engaged in the observation of the avatar's right-arm reaching and grasping the glass. Each action could be correct (C) or erroneous. Erroneous actions were defined as small (SE) or large (LE) depending on their trajectory's deviation from the to-be-grasped glass, with a 5 and 25 cm right-ward arm-path deviation, respectively. Each action lasted 1000 ms and consisted in i) an initial reaching movement toward the glass (700 ms), and ii) a grasping phase in the last 300 ms, in which avatar's arm defined one of the three possible conditions (C, SE, LE). This procedure allowed us to control the onset of the execution error in SE and LE. Then, 3000 ms elapsed after the completion of each action, before the virtual limb returned to its starting position. At this stage, sense of immersivity in the virtual body was assessed by asking participant to verbally rate on a 1–7 Rating Scale (1 = no sensation and 7 = highest sensation): i) how strongly the virtual arm was felt as part of their body and ii) how in control they felt of the virtual arm (for more details, see Supplementary Materials). The EEG task consisted of 200 trials (140 C, 30 SE, 30 LE), arranged in four blocks (50 trials each; ~10 min) separated by three short breaks. The number of SE and LE was the same (30%) for each block, whereas the types of trial were randomized in each block. Before undergoing the EEG task, participants performed a practice session of 14 trials (8 C, 3 SE and 3 LE).