ARTICLE IN PRESS

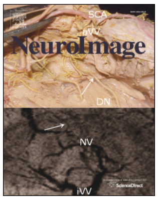
YNIMG-12500; No. of pages: 10; 4C: 2, 5, 6

NeuroImage xxx (2015) xxx–xxx

Contents lists available at ScienceDirect

NeuroImage

journal homepage: www.elsevier.com/locate/ynimg



Violating body movement semantics: Neural signatures of self-generated and external-generated errors

Gonçalo Padrao [a,b,1], Mar Gonzalez-Franco [c,1], Maria V. Sanchez-Vives [b,c,d,e], Mel Slater [c,e,f,2], Antoni Rodriguez-Fornells [a,b,e,*,2]

[a] *Cognition and Brain Plasticity Group [Bellvitge Biomedical Research Institute-] IDIBELL, L'Hospitalet de Llobregat, Barcelona, 08097, Spain*
[b] *Department of Basic Psychology, University of Barcelona, Barcelona 08035, Spain*
[c] *EVENT Lab, University of Barcelona, Barcelona, Spain*
[d] *IDIBAPS (Institut d'Investigacions Biomèdiques August Pi i Sunyer), Barcelona, Spain*
[e] *Catalan Institute for Research and Advanced Studies, ICREA, Barcelona, Spain*
[f] *Department of Computer Science, University College London, London, UK*

ARTICLE INFO

Article history:
Received 9 April 2015
Accepted 9 August 2015
Available online xxxx

Keywords:
Error monitoring
Event-related potential
Body ownership
Agency
Motor control

ABSTRACT

How do we recognize ourselves as the agents of our actions? Do we use the same error detection mechanisms to monitor self-generated vs. externally imposed actions? Using event-related brain potentials (ERPs), we identified two different error-monitoring loops involved in providing a coherent sense of the agency of our actions. In the first ERP experiment, the participants were embodied in a virtual body (avatar) while performing an error-prone fast reaction time task. Crucially, in certain trials, participants were deceived regarding their own actions, i.e., the avatar movement did not match the participant's movement. Self-generated real errors and false (avatar) errors showed very different ERP signatures and with different processing latencies: while real errors showed a classical frontal-central error-related negativity (Ne/ERN), peaking 100 ms after error commission, false errors elicited a larger and delayed parietal negative component (at about 350–400 ms). The violation of the sense of agency elicited by false avatar errors showed a strong similarity to ERP signatures related to semantic or conceptual violations (N400 component). In a follow-up ERP control experiment, a subset of the same participants merely acted as observers of the avatar correct and error movements. This experimental situation did not elicit the N400 component associated with agency violation. Thus, the present results show a clear neural dissociation between internal and external error-monitoring loops responsible for distinguishing our self-generated errors from those imposed externally, opening new avenues for the study of the mental processes underlying the integration of internal and sensory feedback information while being actors of our own actions.

1. Introduction

Humans can be successfully embodied in a surrogate body, either of an avatar (Slater et al., 2010; Banakou et al., 2013) or a robot (Kishore et al., 2014), opening a number of interesting scientific questions. For example, are we able to clearly discriminate whether the origin of an action is due to the intention of the human participant or the surrogate itself? Furthermore, to what extent is our brain able to distinguish self- vs. externally generated erroneous actions which may undermine one's natural sense of agency? Here, we shed light on this issue describing different neurophysiological signatures associated to both types of erroneous actions (self-generated vs. externally imposed errors) in a scenario with embodiment in a full virtual surrogate body.

In normal circumstances, when our ongoing actions and the predicted sensory consequences of these actions (feedback) are coherent, we experience the sensation of agency with respect to our actions ("this action is mine"), and we are typically not even aware of such considerations (Pacherie, 2001; Gallagher, 2005). However, in the case where there is a conflict between the predicted consequences of our actions and their actual consequences (Slachevsky et al., 2001; Haggard and Chambon, 2012), we might detect an agency violation through an error detection mechanism (referred to here as external error-monitoring loop—*E-eml*). This mechanism might be constantly checking whether the final sensory feedback is coherent with expected sensory consequences of our actions, created using an internal (*efference*) copy of our motor commands. These sensory feedback estimations during movement may rely strongly on previous representations of the body in terms of limb position, movement, or posture which normally give us a naturally sense of being the agents of our actions (Giummarra et al., 2008). In the case of a mismatch

---

* Corresponding author at: Department of Basic Psychology, University of Barcelona (ICREA-IDIBELL), Barcelona, Spain.
E-mail address: antoni.rodriguez@icrea.cat (A. Rodriguez-Fornells).

[1] Both authors *contributed equally* to the present study.

[2] Both authors *share co-senior authorship*.

http://dx.doi.org/10.1016/j.neuroimage.2015.08.022
1053-8119/© 2015 Published by Elsevier Inc.

Please cite this article as: Padrao, G., et al., Violating body movement semantics: Neural signatures of self-generated and external-generated errors, NeuroImage (2015), http://dx.doi.org/10.1016/j.neuroimage.2015.08.022

in this comparison between expected and actual sensory feedback outcomes, a disruption of the sensation of agency might be elicited (Synofzik et al., 2008).

While this *E-eml* might be constantly checking the congruency between our external and internal worlds, a concurrent internal and rapid error detection mechanism evaluates whether our ongoing motor plans are correct, implementing very fast corrective actions in order to prevent and abort the production of erroneous responses. Several models have proposed that an internal forward signal – *efference copy* – is used to generate constant predictions of the consequences of our actions which are used to compute error deviations from the expected goal even before the action has been completed (Holst and Mittelstaedt, 1950; Wolpert and Miall, 1996; Jeannerod, 2006; Crapse and Sommer, 2008). This *internal error-monitoring loop* (*I-eml*) has been associated with the *error-related negativity* or *error negativity* (Ne/ERN), an event-related potential (ERP) component appearing approximately 60 ms after the commission of a real error (Falkenstein et al., 1990, 1991; Gehring et al., 1993; Rodriguez-Fornells et al., 2002; Holroyd et al., 2005) and elicited in the anterior cingulate cortex (Ullsperger and von Cramon, 2001; Holroyd et al., 2004; Marco-Pallarés et al., 2008).

Even though these two error detection mechanisms – *E-eml* and *I-eml* – rely on similar representations (both rely on the efference copy), the computations that each performs involve access to different types of feedback information. The main aim of the present research was to functionally dissociate the neurophysiological mechanisms underlying the external and the internal EML. To accomplish this goal we performed two ERP experiments. In Experiment 1, we recorded for first time ERPs in healthy participants embodied in a virtual body (Slater et al., 2010) while they carried out an error-prone reaction time task (Rodriguez-Fornells et al., 2002) in a fully immersive virtual environment (IVE) (see Fig. 1a and Movie 1 in Supplementary Material). Critically, on a few occasions, participants' correct responses were falsified by an "erroneous" movement of their embodied avatar (i.e., avatar errors), which perturbed their sense of agency. ERP signals related to self-generated errors and avatar errors were then compared. While the elicitation of the ERN component was expected for self-generated errors (as a reflection of the *I-eml*), no specific prediction was made regarding externally generated (virtual body) errors. Experiment 2 was carried out in order to rule out the possibility that the ERP effects observed in Experiment 1 for external-generated errors could have been due to the mere observation of a virtual human performing a wrong action rather than the output of the external-error-monitoring loop (*E-eml*).

2. Materials and methods

2.1. Participants

Eighteen neurologically healthy right-handed volunteers from the Faculty of Psychology at the University of Barcelona participated in the first experiment (Experiment 1) (6 men; mean age, 26 ± 7 years). Two weeks after the participation in the main experiment, nine participants (3 men; mean age, 25 ± 8 years) agreed to return to the lab to participate in a control experiment (Experiment 2). All gave written informed consent according to the declaration of Helsinki and were paid for their participation. The ethical committee from the University of Barcelona gave approval to the project (Institutional Review Board IRB 00003099).

2.2. Apparatus

Participants were fitted with a stereo NVIS nVisor SX111 head-mounted display (HMD). This has dual SXGA displays with 76°H × 64°V degrees field of view (FOV) per eye, totaling a wide field of view 111° horizontal and 60° vertical, with a resolution of 1280 × 1024 per eye displayed at 60Hz. Head tracking was performed by a 6-degrees of freedom (DOF) Intersense IS-900 device.

A gender-matched virtual body (or avatar) was displayed from a first person perspective (1PP) with respect to the virtual body's eyes, so that it visually substituted the real body of the participant (see Fig. 1; see also Movie 1 at the Supplementary Material). The position of the participants' real hand was tracked using an optical infrared system (12 camera OptiTrack). The whole arm kinematics (hand, elbow, and shoulder positions and rotations) were computed from the hand position using inverse kinematics. Our setup supported the real-time display of the avatar with 6 DOF in the head and 4 DOF in the right arm giving the participant strong visual–motor coherence between real and virtual right-arm movements. The virtual environment was programmed in the XVR system (Tecchia et al., 2010) and the virtual character displayed through the HALCA library (Gillies and Spanlang, 2010; Spanlang et al., 2014).

2.3. Procedure

2.3.1. Experiment 1

Participants performed a standard error-prone Eriksen flanker attention task (Rodriguez-Fornells et al., 2002) and were required to

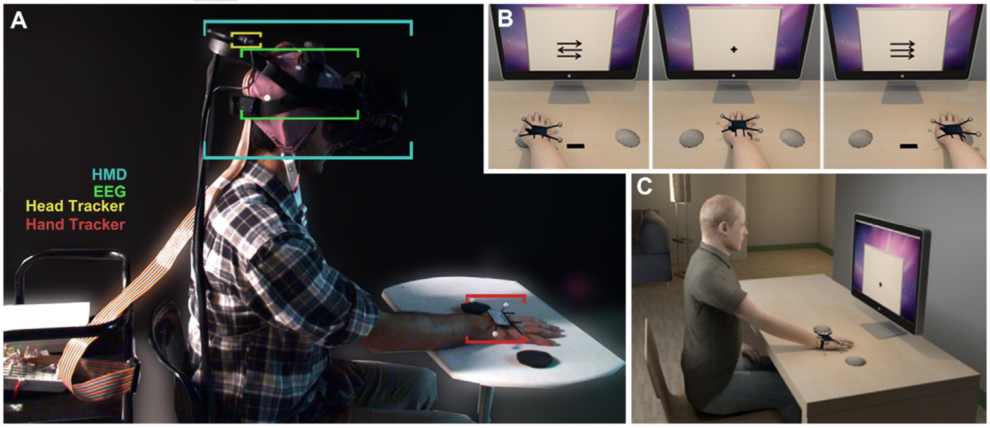


Fig. 1. Experimental design used in Experiment 1. (A) Participant in the laboratory with the head-mounted display (HMD), electroencephalography (EEG), and the head and hand tracking systems. (B) First person perspective (1PP) of the virtual arrow flanker task. Participants were instructed to perform fast movements with the right hand in the direction of the central arrow. After each movement, the hand returned to the starting position (middle panel). The virtual hand followed the tracked real hand, but in some trials the displayed virtual hand movement was incongruent (InCM) with the participants' real movements, thus generating an "false(avatar) error." Three conditions were relevant for the EEG analysis, correct responses, real errors, and false errors. (C) Gender-matched avatar of the participant in the immersive virtual environment (IVE).

Please cite this article as: Padrao, G., et al., Violating body movement semantics: Neural signatures of self-generated and external-generated errors, NeuroImage (2015), http://dx.doi.org/10.1016/j.neuroimage.2015.08.022