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Contextualizing action observation in the predictive brain: Causal contributions of prefrontal and middle temporal areas

Lucia Amoruso [a,c,*], Alessandra Finisguerra [b], Cosimo Urgesi [a,b]

[a] Laboratory of Cognitive Neuroscience, Department of Languages and Literatures, Communication, Education and Society, University of Udine, Udine, Italy
[b] Scientific Institute, IRRCS Eugenio Medea, Pasian di Prato, Udine, Italy
[c] Basque Center on Cognition, Brain and Language, San Sebastian, Spain

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ABSTRACT

Context facilitates the recognition of forthcoming actions by pointing to which intention is likely to drive them. This intention is thought to be estimated in a ventral pathway linking MTG with frontal regions and to further impact on the implementation of sensory predictions within the action observation network (AON). Additionally, when conflicting intentions are estimated from context, the DLPFC may bias action selection. However, direct evidence for the contribution of these areas to context-embedded action representations in the AON is still lacking. Here, we used a perturb-and-measure TMS-approach to disrupt neural activity, separately in MTG and DLPFC and subsequently measure cortico-spinal excitability while observing actions embedded in congruent, incongruent or ambiguous contexts. Context congruency was manipulated in terms of compatibility between observed kinematics and the action goal suggested by the ensemble of objects depicted in the environment. In the control session (vertex), we found an early facilitation and later inhibition for kinematics embedded in congruent and incongruent contexts, respectively. MTG stimulation altered the differential modulation of M1 response to congruent vs. incongruent contexts, suggesting this area specifies prior representations about appropriate object graspability. Interestingly, all effects were abolished after DLPFC stimulation highlighting its critical role in broader contextual modulation of the AON activity.

Introduction

Observing other people's actions involves the activation of a set of frontal, parietal, and temporal areas collectively termed the Action Observation Network (AON), which are thought to underpin our ability to perceive and comprehend others' behaviors (Caspers et al., 2010; Grafton, 2009). Evidence from neuroimaging studies (Buccino et al., 2004; Calvo-Merino et al., 2005) shows that activity within this network is modulated by the observer's ability to perform the movements. Furthermore, transcranial magnetic stimulation (TMS) studies show that this activity replicates the muscular involvement (Alaerts et al., 2009; Fadiga et al., 1995; Urgesi, Candidi, Fabbro, Romani and Aglioti, 2006a) and temporal profile of the observed action (Borroni et al., 2005; Gangitano et al., 2001; Urgesi et al., 2010), thus pointing to the existence of a motor resonance mechanism that maps observed movements onto one's own action representations. Yet, at a mechanistic level this proposal is not trivial: how do we understand others' intentions by simply observing their movements? Originally developed in the domain of basic visual perception, predictive coding framework provides an explanation to this controversial question (Kilner et al., 2007).

The core proposal of predictive coding in the action domain is that forward models, which are used in action execution to predict the expected sensory consequences of our own movements (Wolpert and Flanagan, 2001; Wolpert and Miall, 1996), can be inverted and used to infer other people's actions. This inferential processing relies on a hierarchical action representation architecture (Grafton and Hamilton, 2007) that involves different levels: (i) muscle, which codes for the pattern of muscular activity required to execute the action (e.g., activation of flexion-extension synergies); (ii) kinematics, which maps the movements of the effectors in space and time (e.g., precision vs. whole hand grasping); (iii) goal, which includes the short-term transitive or intransitive aim (e.g., bringing an object toward vs away from the body); and (iv) intention, which includes the long-term purpose behind the action (e.g., eating vs. offering). Thus, given the observer's prior about other's likely intention/goal, the AON predicts the more concrete aspects levels of action representation (such as motor commands and perceptual

* Corresponding author. Laboratory of Cognitive Neuroscience, University of Udine, Via Margreth, 3, I-33100 Udine, Italy.
E-mail address: lucia.amoruso@uniud.it (L. Amoruso).

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kinematics) on the basis of the observer's own motor representations. If the comparison between the predicted and the observed sensory information mismatches, a prediction error is generated and used to update action representation at the different levels of the cortical hierarchy. By reducing the prediction error at all levels of action representation, the most likely cause of the action can be inferred. Although this model offers an elegant explanation of how actions are recognized, it creates a new difficulty: where is the prior representation of others' intention generated?

While previous brain stimulation studies have mainly assessed the functional relevance of the AON to action perception (Pobric and Hamilton, 2006; Tidoni et al., 2013; Valchev et al., 2017; Avenanti et al., 2013), evidence on how the AON interacts with higher-order areas is scanty. It has been proposed (Kilner, 2011) that others' intentions are inferred from the context along a ventral pathway (in brain areas outside of the AON) linking the posterior middle temporal gyrus (pMTG) with the more anterior regions of the inferior frontal gyrus. Briefly, this pathway would be involved in retrieving semantic information related to the observed object and associated actions, as well as in the selection, given the intention, of the more likely action representation. The selected representation would then impact on the classical dorsal AON responsible for the encoding of the concrete motor parameters about upcoming movements.

In a series of previous studies (Amoruso et al., 2016; Amoruso and Urgesi, 2016), we combined single-pulse TMS and motor-evoked potentials (MEPs) recording to explore whether top-down contextual information was capable of modulating action coding at lower levels of representation (i.e., muscle and kinematics). We recorded MEPs from the FDI and a control muscle while participants watched videos depicting everyday actions embedded in congruent, incongruent or ambiguous contexts. Videos were interrupted before action ending and participants were requested to predict action unfolding. Context-action congruency was manipulated in terms of compatibility between observed grasping kinematics and the setting in which the action was observed. For instance, one of these settings depicted a mug full of coffee and a plate with some biscuits (breakfast scenario). If the observed model grasped the mug by its handle with a precision grip, this condition was coded as congruent. However, if the model grasped the mug using a whole-hand grip from the top, this was coded as incongruent, given that this type of grasping prevented the model from drinking in a context were the highly expected action was “to drink”. After the video, two possible descriptors (i.e., to drink and to move) were presented and participants had to select which was the actor's more likely intention, given contextual and kinematics information present in the video. In addition, we used ambiguous contexts where both type of actions and associated grasping movements were equally plausible (i.e., a mug half full of coffee). We found that, as compared to the ambiguous condition, congruence between the observed movements and the contextual setting facilitated the motor cortex at early stages (~240 ms after action onset), while incongruence between them resulted into a later inhibition (~400 ms after action onset). Overall, these results were interpreted as reflecting predictive processing in M1, triggered by areas outside the AON. We reasoned that this paradigm suited well for testing where context-based priors might be generated since it allows the manipulation of contextual information in terms of its compatibility with the forthcoming movements. Furthermore, the different timing and mechanisms of the observed effects (i.e., early facilitation and later inhibition) suggested that they might reflect signals connecting the AON with two different pathways. The first pathway, likely involving pMTG (Kilner, 2011), may mediate the generation of context-based expectations and lead to the congruence facilitation effect at an early time window, namely around 240 ms, when muscle-specific motor resonance responses are observable in M1 (Barchiesi and Cattaneo, 2013; Naish et al., 2014). The other pathway may be involved in detecting interference and inhibiting disconfirmed action representations in M1 based on contextual information. A likely candidate involved in this later pathway is the prefrontal-premotor route. Evidence from primates studies (Cai and Padoa-Schioppa, 2014; Saleem et al., 2014; Takahara et al., 2012; Tsujimoto et al., 2011) suggests that top-down signals from the dorsolateral prefrontal cortex (DLPFC) bias action selection in premotor regions. In a similar vein, action selection theories suggest that, when alternative representations compete for further processing in the AON, the DLPFC biases action selection towards context-relevant information (Cisek, 2006, 2007). Furthermore, there is evidence that the DLPFC might be specifically involved in providing top-down signal when anomalies in action representation within a semantic context are detected (Balconi and Vitaloni, 2012, 2014). Thus, the DLPFC seems to be the best candidate for mediating the late inhibition of motor facilitation when actions are observed in incongruent contexts (Amoruso et al., 2016).

However, it is worth mentioning that recent studies provide evidence for the involvement of the DLPFC in the early generation of top-down predictions about object's identity (Calderone et al., 2013; Kveraga, Boshyan and Bar, 2007a), motion direction (Rahnev et al., 2011) and, interestingly, context-based action recognition (Maranesi et al., 2014). Thus, an alternative possibility is that the DLPFC would play a more general and pervasive role in building-up context-based predictions of others' actions rather than being only recruited in the presence of semantic anomalies.

Here, we aimed to study the functional contribution of two brain nodes beyond the AON in the motor representation of context-embedded actions. Specifically, we tested the involvement of left pMTG and DLPFC in the generation of context-based expectations and in the inhibition of conflicting action representations, respectively. We used a perturb-and-measure transcranial magnetic stimulation (TMS) approach, which offers the unique possibility to i) transiently disrupt neural activity in regions of interest using off-line continuous theta burst stimulation (cTBS) and to ii) measure the consequent functional modulation of corticospinal excitability (CSE) to observed actions via online single-pulse TMS of M1. This approach, originally developed by Avenanti et al. (2007) has been used in various previous studies (Arfeller et al., 2013; Avenanti et al., 2013; Enticott et al., 2012; Ubaldi et al., 2015; Valchev et al., 2016) in order to assess the role of brain areas belonging to the classical AON and their contribution to motor resonance. To the best of our knowledge, this is the first study in using this approach to test the involvement of brain areas beyond the AON (MTG and DLPFC) and examine their potential contribution to early/late context-dependent motor resonance responses.

We hypothesized that, if the pMTG (Kilner, 2011) and/or DLPFC (Maranesi et al., 2014) are involved in the generation of context-based expectations about others' intentions during action observation, then, by interfering with its activity, both the facilitation and inhibition of CSE for congruent and incongruent contexts, respectively, should be abolished (H1). In a similar vein, if the DLPFC is involved in solving conflicts between action representations (Balconi and Vitaloni, 2012, 2014), only the inhibitory effect previously observed for incongruent contexts, but not the facilitatory one for congruent contexts, should be disrupted when altering its activity (H2).

Materials and methods

Participants

A total of eighteen participants (10 women; M = 22.11, SD = 2.89) recruited at the University of Udine took part in the study. One male participant was removed from the analysis due to technical problems during data acquisition, thus all analyses were carried out in a sample of seventeen subjects. Participants were all right-handed according to the Standard Handedness Inventory (Briggs and Nebes, 1975), had normal acuity in both eyes and were free from any contraindication to TMS (Rossi et al., 2009). They gave written informed consent prior to experimentation and received course credits for participation in the study. The experimental procedures were approved by the local Ethics Committee (Comitato Etico Regionale Unico, Friuli Venezia Giulia, Italy) and were