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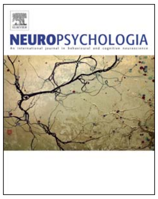

Predictability of action sub-steps modulates motor system activation during the observation of goal-directed actions

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ABSTRACT

Action perception and execution are linked in the human motor system, and researchers have proposed that this action-observation matching system underlies our ability to predict observed behavior. If the motor system is indeed involved in the generation of action predictions, activation should be modulated by the degree of predictability of an observed action. This study used EEG and eye-tracking to investigate whether and how predictability of an observed action modulates motor system activation as well as behavioral predictions in the form of anticipatory eye-movements. Participants were presented with object-directed actions (e.g., making a cup of tea) consisting of three action steps which increased in their predictability. While the goal of the first step was ambiguous (e.g., when making tea, one can first grab the teabag or the cup), the goals of the following steps became predictable over the course of the action. Motor system activation was assessed by measuring attenuation of sensorimotor mu- and beta-oscillations. We found that mu- and beta-power were attenuated during observation, indicating general activation of the motor system. Importantly, predictive motor system activation, indexed by beta-band attenuation, increased for each action step, showing strongest activation prior to the final (i.e. most predictable) step. Sensorimotor activity was related to participants' predictive eye-movements which also showed a modulation by action step. Our results demonstrate that motor system activity and behavioral predictions become stronger for more predictable action steps. The functional roles of sensorimotor oscillations in predicting other's actions are discussed.

1. Introduction

It is well established that actions and their observations are tightly linked in the human motor system. Activation of the motor system can be observed not only during action execution but also during action observation (Cochin et al., 1999; Hari, 2006; Lepage and Théoret, 2006). Researchers have proposed that this action-observation matching system facilitates our ability to predict observed behavior (Kilner et al., 2007; Palmer et al., 2016a; Prinz, 2006; Schubotz, 2007). It is argued that the outcome of an observed action can be inferred and predicted through a mapping of observed actions onto own motor representations (Rizzolatti and Sinigaglia, 2016). In line with a predictive function of the motor system, studies have shown that the knowledge of an upcoming action elicits motor system activation already prior to the action onset (Kilner et al., 2004; Southgate et al., 2009). Additional support for a matching between observed actions and own motor representations comes from studies using eye-tracking. Flanagan and Johansson (2003) measured participants eye-movements during the performance and observation of a block stacking task. They discovered that participants preceded goal-directed hand movements with their gaze in a highly similar manner during both the action execution and action observation condition. Anticipatory eye-movements during action observation have since been reported in multiple studies (Elsner et al., 2012; Falck-Ytter et al., 2006; Gredebäck and Falck-Ytter, 2015; Hunnius and Bekkering, 2010) and it is argued that these behavioral predictions are generated due to the activation of the corresponding action plans in the observers' motor system (Flanagan and Johansson, 2003). Elsner et al. (2013) recently used transcranial magnetic stimulation (TMS) to directly test this hypothesis. They showed that stimulation of the motor cortex slowed predictive eye-movements during an action observation task, providing evidence that the motor system is indeed involved in the generation of anticipatory eye-gaze.

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Many studies have made use of EEG and MEG recordings using attenuation of central oscillatory power in the mu- and beta-frequency range as a marker of motor system activation (McFarland et al., 2000; Muthukumaraswamy and Johnson, 2004; Perry et al., 2010; Pfurtscheller, 1981; Denis et al., 2016; Koelewijn et al., 2008; McFarland et al., 2000; Meyer et al., 2015). In agreement with a predictive function of the motor system (Kilner et al., 2007), studies have shown that sensorimotor oscillations are modulated during the observation of erroneous or unexpected actions (Koelewijn et al., 2008; Meyer et al., 2015; Stapel et al., 2010). Stapel et al. (2010) found, for instance, that 12-month-old infants demonstrated greater mu-attenuation when observing unusual actions upon everyday objects (such as bringing a cup to the ear rather than to the mouth) compared to actions usually associated with these objects. The researchers argued that observing actions which deviate from the initially expected trajectory requires the generation of additional predictions which is consecutively reflected in enhanced activation of the motor system (Kilner et al., 2007; Stapel et al., 2010). Similarly, in adults, observing erroneous rather than correct actions has also been shown to elicit increased motor system activation, in particular in the beta-frequency range (Koelewijn et al., 2008; Meyer et al., 2015). Interestingly, several other studies have recently also suggested a relationship between beta-oscillations and predictive processing (Palmer et al., 2016b; Tan et al., 2016; van Pelt et al., 2016). Tzagarakis et al. (2010), for example, showed that beta-band desynchronization during motor preparation was modulated by the uncertainty of movement direction in an instructed delay-reaching task. More specifically, beta-power was found to be lower when the target location was more predictable. Similarly, Tan et al. (2016) modulated the uncertainty of the forward model parameters in a visuomotor adaptation task and showed that post-movement beta synchronization was modulated by this uncertainty. Taken together, these studies suggest that sensorimotor beta-oscillations may be reflective of the motor systems' predictive processing and in particular related to the precision of predictions (Palmer et al., 2016b).

Altogether, there is strong empirical support for the notion that the motor system is involved in the generation of predictions about observed actions (Elsner et al., 2013; Kilner et al., 2007, 2004; Southgate et al., 2009). To date, however, most studies investigating action prediction made use of simple one-step goal-directed actions, like moving a ball into a bucket (Falck-Ytter et al., 2006) or bringing a cup to the mouth (Hunnius and Bekkering, 2010). Actions we encounter during everyday life, on the other hand, consist of multiple sub-actions that depend on each other and need to be executed in a particular sequence in order to achieve an overall action goal. For example, to make a cup of tea, one first grabs a teabag, then puts it in a cup and in the last step, fills the cup with hot water. In such a multi-step action, the distinct action steps depend on each other and while the first step is often ambiguous (one can first grab the teabag or the cup), the later steps become more predictable over the course of the action (once the tea bag has been put into the cup the only missing step in making tea is pouring hot water into the cup). Although it has been established that the motor system shows predictive activation during the observation of simple one-step actions (Kilner et al., 2004; Southgate et al., 2009), it remains unknown whether and in which way activity is also modulated by the predictability of distinct action steps within a multi-step action sequence. A first indication that the predictability of an action step influences action prediction comes from a recent study by Poljac et al. (2014). In their action observation paradigm, participants' eye movements were registered, while they watched object-directed actions consisting of three distinct action steps which increased in predictability (such as making a cup of tea). The researchers showed that over the course of the different action steps, predictive eye-movements towards the goal of the next action step became more frequent and rapid. These findings were interpreted as evidence that the sub-actions are not processed in isolation, but that the semantic information from the distinct action steps is accumulated, facilitating the generation of predictions about the later steps of the observed action. Since their study focused on behavioral measures of predictions only, the role of the motor system in the integration of semantic information in multi-step actions remains to be investigated.

The present study examined neural markers of action prediction during the observation of multi-step actions. We tested the hypothesis that predictive motor system activation is modulated by the predictability of the distinct steps in multi-step actions reflecting the integration of information as the action unfolds. In a combined EEG and eye-tracking study, we measured motor system activation along with predictive eye-movements while participants were observing different object-directed multi-step actions (similar to Poljac et al., 2014). For each action, the goal of the first step was ambiguous whereas the later steps became more predictable over the course of the action. Motor system activation was assessed by examining attenuation of central mu- and beta-frequency power. Based on the predictive role of the motor system (Kilner et al., 2007, 2004; Southgate et al., 2009), we expected to find a step-wise increase of motor system activation, indexed by attenuation of sensorimotor oscillations -in particular in the beta-frequency range-, mirroring the increased predictability of the distinct action steps. Following Poljac et al. (2014), we hypothesized a similar modulation of predictive eye-movements. Moreover, we expected a relationship between the neural and behavioral measures of action prediction, reflecting the tight link between the motor system and predictive eye-movements that has previously been established (Elsner et al., 2013).

2. Methods

2.1. Participants

In total, 31 participants (age: $M = 23.32$, $SD = 3.06$; 21 female) took part in the study. From this set, 28 were included in the EEG data analysis (age: $M = 23.04$, $SD = 3.09$; 19 female) and 22 participants were included in the eye-tracking data analysis (age: $M = 23.17$, $SD = 3.08$; 14 female). Nineteen participants (age: $M = 22.78$, $SD = 3.10$; 12 female) contributed data to both the EEG and eye-tracking datasets and were included in the correlation analysis of the two measures. Participants were all healthy adults, who signed informed consent and received course credits or monetary compensation for their participation. All but one participants were right handed and all participants had normal or corrected to normal vision and hearing.

For the EEG analysis, two participants were excluded due to technical problems and one participant was excluded due insufficient number of artifact-free trials. The relatively large number of participants excluded from the eye-tracking analysis was due to equipment problems ($n = 5$) or an insufficient amount of valid trials for each of the three conditions ($n = 4$). For one participant, behavioral data to confirm proper attention to the stimulus display (see below) was not collected due to technical problems.

2.1.1. Stimulus material

For the purpose of the study, video recordings were created of a female actor sitting at a table performing a three-step action using everyday objects (see Fig. 1). Each video lasted for approximately 15 s and started with the actor sitting in a neutral position with her hands placed on the table. During each video, there were three objects situated on the table, one at both sides of the actor and one in the middle in front of the actor. After approximately 2 s, the actor started moving her hand towards the first object (Step1). She then picked up the first object and brought it towards the second object (Step2) where usually a short action was performed. Then the actor continued to the last object (Step3) to finalize the overall action. An example of such an action is given in Fig. 1.

The actions were chosen such that the initial action step was ambiguous, whereas the last step followed deterministically from the two