

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



Fig. 1. Stimulus Examples. Two example stimulus are displayed in part A. The actor in the upper example first grasps the spoon (Step1), brings it to the sugar pot (Step2), scoops sugar, and finally brings the spoon to the coffee cup (Step3). In the lower example, the actor first gets the cheese slicer (Step1), brings it to the cheese (Step3), slices off a piece of cheese, and finally brings the piece to her mouth (Step3). The corresponding Areas of Interest (Aols) of the three goal locations from the two example stimulus videos can be seen in part B.

previous steps of the sequence. Start, middle, and end locations of the action steps were counterbalanced so that participants were unable to predict the next step solely based on the object location. Also, the actor's eyes and a large part of her face were covered by the brim of a black hat to ensure that participants were unable to predict the upcoming action step based on the actor's gaze. Actions were similar to the ones used by Poljac et al. (2014), but new material was recorded to enlarge the stimulus set so that sufficient trials could be presented required for the EEG analysis. In line with the original stimulus set, about half (13) of our final 28 videos ended at the mouth or face of the actor and the other half (15) ended at an object on the table. In addition to these experimental videos, eight catch videos were recorded in which the last action step did not lead to the conclusion of the overall action goal (see Supplementary Fig. 1 for an example). After the presentation of a catch video, and after 16 pseudo-randomly selected experimental videos, participants were asked to indicate whether the observed action was performed correctly. Participant's answers were analyzed to ensure that they were paying attention to the stimulus presentation.

2.1.2. Stimulus presentation

Stimulus presentations and communication with the EEG and eye-tracking systems was realized using Presentation® software (Version 18.1.06.09.15, Neurobehavioral Systems Inc., Albany, CA, USA).

All participants saw each video (catch and experimental) twice during the experiment, resulting in a total of 72 trials which were presented in a pseudo-random order. There were four blocks during which 18 trials were presented on a 24-in. monitor located in a shielded experimental room. Each trial started with the presentation of a baseline period in which a fixation cross was displayed for 1250 ms on average (\pm 250 ms). Then an experimental video or a catch video was presented. After each catch trial and after 16 pseudo-randomly selected experimental trials, participants were asked to indicate whether the observed action was performed correctly. Responses were recorded using a button box. The entire experiment lasted for about half an hour and after each of the four blocks participants were able to take a short break and continue the experiment whenever they were ready.

2.1.3. EEG recordings

EEG was recorded using 64 Ag/AgCl active electrodes placed in actiCaps (Brain Products, Munich, Germany) and arranged according to the 10–20 system. Fifty-nine electrodes were used for scalp recordings, four electrodes recorded vertical and horizontal EOG and one electrode was placed on the left mastoid for potential additional reference. Data was collected using BrainVisionRecorder (Brain Products, Munich, Germany) with the right mastoid as online reference and a sampling rate of 1000 Hz. Impedances were kept below 10 kOhm and data was monitored throughout the session by the experimenter.

2.2. Eye-tracking recordings

Eye-movements were recorded using an SMI RED500 stand-alone eye-tracker and the iView X™ SDK 3.0 software (SensoMotoric Instruments GmbH, Teltow, Germany) with a sampling rate of 250 Hz. The eye-tracker was calibrated using a 9-point calibration at the start of the experiment. Eye- and head-position were monitored throughout task by the experimenter.

2.3. Data analysis

2.3.1. EEG data analysis

EEG data was analyzed using MATLAB (2013b, The MathWorks Inc., Natick, MA, 2000) and Fieldtrip (Oostenveld et al., 2011), an open source toolbox for EEG data analysis.

2.3.1.1. Data segmentation. Data were read into Fieldtrip and segments were created for the three action steps per video and for the baseline period. Action step segments had a duration of 1200 ms but a variable onset depending on the particular stimulus video. The timing of the segments was defined for each stimulus video separately and was based on the same segmentation as used in the eye-tracking analysis (see Analysis of eye-movement data section). The moment when the actor's hand first entered the Area of Interest surrounding the goal of that action step represented the end of the EEG action step segment. The beginning of the EEG action step segment was consecutively determined as 1200 ms prior to the end point. Baseline period

segments had a duration of 1000 ms and were locked to fixation cross onset.

2.3.1.2. Preprocessing and artifact rejection using ICA. In a first step of cleaning and preprocessing the data, extremely noisy or flat channels as well as trials containing excessive artifacts were removed from the data by visual inspection. For 18 participants, no channels were rejected. For the remaining 10 participants, on average two channels were rejected (ranging from one to four, see [Supplementary Table 1](#)) but this never included channel Cz. In a following step, Independent Component Analysis (ICA) was performed in order to extract artifacts caused by eye-movements and eye-blinks. First, ICA components were correlated with the data from the bipolar EOG channels. Consecutively, the spatial distribution of each component was inspected visually and in a last step the time course was visually assessed and components were manually rejected. For all but one participants, at least two components were rejected that correlated highly with the EOG data and showed a specific spatial distribution and time course associated with ocular artifacts. For the remaining participant only one component could be identified. In addition, for five participants an additional component was rejected which either also matched the criteria for ocular artifacts ($n = 1$) or clearly reflected the heart rate throughout the experiment ($n = 4$). After determination and removal of the ICA components, the data was reconstructed and further analyzed. Previously excluded channels were interpolated using a nearest neighbor approach and finally, the data was re-referenced to the average of all electrodes. In a last step, each segment was visually screened and segments containing remaining artifacts were excluded manually from further analysis.

Trials for the fixation and the three action steps were then separated for analysis of spectral power. For one participant the amount of artifact-free baseline period segments was extremely low ($n = 17$) and this participant was hence excluded from further analysis. On average the included participants contributed 49.21 ($SD = 3.73$) trials to Step1, 48.57 ($SD = 4.09$) trials to Step2, 49.43 ($SD = 4.01$) trials to Step3, and 43.25 ($SD = 5.88$) trials to the baseline period.

2.3.1.3. Calculation of spectral power. To calculate the spectral power of the signal, Fast Fourier Transform was applied to the segments using a multitaper frequency transformation. In order to control for individual differences, the resulting power values of the three action steps were normalized for each individual participant using the power values from the baseline period segments. This was achieved by dividing the power from each action step by the power of the baseline period and taking the log of this ratio. This is a common way of normalizing frequency power data (see, for example, [Cuevas et al., 2014](#); [Meyer et al., 2015](#)).

Based on previous literature, our measure for the activation of the motor system activation during action observation was the attenuation of the central mu- and beta-frequency power. EEG power was extracted from Cz and mu- and beta-band ranges were set from 8 to 12 Hz (mu) and 15–25 Hz (beta) (see: [Brinkman et al., 2014](#); [McFarland et al., 2000](#); [Meyer et al., 2015](#); [Perry et al., 2010](#); [Pfurtscheller, 1981](#); [Pineda, 2005](#); [Denis et al., 2016](#)). All analyses were performed on the log transformed normalized power values. To investigate whether the power in the mu- and beta-frequency range was attenuated during action observation with respect to baseline period, one-sample *t*-tests were conducted for each of the action steps and frequency ranges. To test for power differences between the three action steps a repeated measures ANOVA with Step as a within-subject factor was conducted for each of the two frequency ranges.

2.3.2. Analysis of eye-movement data

2.3.2.1. Determination of Areas of Interest (AoI). Raw eye-movement data was read into BeGaze™ 3.0 analysis software (SensoMotoric Instruments GmbH, Teltow, Germany) where fixations were extracted based on the standard filter settings (minimum fixation duration of 50 ms and peak velocity threshold of 40°/s). For each experimental

video three rectangular-shaped Areas of Interest (AoIs) were defined around each of the goal objects of the three action steps. AoI size varied per video ($M = 30698.07$ pixels, $SD = 24404.31$), but the average AoI size did not differ between the three action steps ($F(2,81) = 1.431$, $p = 0.245$). Finally, fixation data for the three AoIs over all experimental trials were extracted and further processed using MATLAB (2012b, The MathWorks Inc., Natick, MA, 2000).

2.3.2.2. Determining Time Windows of Interest (TWoI). For each experimental video, a predictive (pTWoI) and reactive time window of interest (rTWoI) was determined for each action step. The moment when the actor's hand started to move towards the goal object was the start of the pTWoI. Conversely, the moment when the actor's hand first entered the goal AoI was used as the end of the pTWoI and the beginning of the rTWoI, respectively. Finally, the end of the rTWoI was selected such that the reactive and predictive window were of equal length.

Due to the fact that natural stimuli were used, TWoI size ($M = 1306.65$ ms, $SD = 331.26$) differed between stimulus videos ($F(2,81) = 18.96$, $p < 0.001$) and window size was on average smaller for Step1 compared to Step2 ($t(27) = -6.72$, $p < 0.001$) and Steps3 ($t(27) = -5.35$, $p < 0.001$), but equal for Step2 and Step3 ($t(27) = 0.41$, $p = 0.685$). To control for differences in TWoI length, we used relative measures for our eye-tracking analysis where possible: For the Looking Time a percentage was used, and for the Count Ratio the number of fixations during the pTWoI were divided by the number of fixations during the pTWoI and rTWoI combined (see below). The segments used in the EEG analysis were always equally long (see EEG analysis) leaving no bias for a particular action step.

2.3.2.3. Classification of predictive and reactive trials. In MATLAB, for each action step, trials were classified as either being predictive (a goal fixation was made during the pTWoI), reactive (no predictive fixation was made, but a goal fixation was made during the rTWoI) or invalid (no goal fixation was made during either TWoI). Participants with less than 15 valid trials per action step were excluded from the analysis. This concerned four individuals from the initial 31 participants who took part in the experiment. On average, the included participants contributed 29.91 ($SD = 9.42$) trials to Step1, 37.77 ($SD = 9.01$) trials to Step2, and 27.14 ($SD = 7.55$) trials to Step3.

2.3.2.4. Calculation of the dependent measures. Similar to [Poljac et al. \(2014\)](#), three measures of interest were calculated separately for each action step: Predictive Looking Time, Predictive Gaze Onset, and Predictive Count Ratio. *Predictive Looking Time* was calculated by extracting the duration of fixations to the AoI during the pTWoI. Looking times were then standardized as a percentage with respect to the length of the respective pTWoI and then averaged over trials for each participant. *Predictive Gaze Onset* was defined as the onset of the first fixation to the AoI relative to the end point of the pTWoI. A larger value hence reflects an earlier onset of the predictive fixation. Finally, the *Predictive Count Ratio* was determined by dividing the number of predictive trials by the total number of trials for each action step. To assess differences in predictive eye-movements for the three action steps, we performed a Repeated measures ANOVA for each of the three dependent measures with Step as a within-subject factor.

2.3.3. Correlation of EEG and eye-tracking measures

To assess the relationship of predictive cortical motor system activation and predictive eye-movements, we performed a correlation analysis. For this purpose, difference scores were derived for all dependent measures reflecting the difference in prediction between two neighboring action steps. More specifically, we subtracted Step1 from Step2, and Step2 from Step3. A more negative difference score in the EEG measure thus reflected less power- and hence more motor system activation- for the later compared to earlier action steps. For the eye-

tracking data, conversely, a larger difference score would reflect enhanced prediction in later compared to earlier action steps. Correlations between EEG-power in the mu- and beta-band with the three eye-tracking measures were calculated separately for each of the two action step contrasts.

3. Results

3.1. Attention to stimulus presentation

Participants answered the questions presented after catch and selected experimental trials correctly 94.48% of the time ($SD = 0.05$), with no differences in performance for catch compared to experimental trials ($t(29) = 0.09, p = 0.929$). This confirmed that participants were paying attention during stimulus presentation.

3.2. EEG results

To assess whether the power in the mu- and beta-frequency range was attenuated during action observation, we conducted a one-sample t -test for each of the action steps separately. As expected, the averaged log ratio of the power was negative in all cases and significantly different from zero for all action steps for the mu-frequency range and the second and third action step for the beta-frequency range ($t(27) < -3.29, ps < 0.004$ for all five contrasts, see [Supplementary Table 2](#) for an overview of the exact test statistics and effect sizes). In addition, the first action step for the beta-frequency range reached marginal significance ($t(27) = -2.02, p = 0.054$). These results showed that for both the mu- and the beta-frequency range, power was attenuated during the action observation periods compared to the baseline period. Next, we assessed differences between the three action steps using a repeated measures ANOVA. No effect of Step was found for the mu-frequency band ($F(2,54) = 1.92, p = 0.156$, see [Supplementary Fig. 2](#) for a visualization of mu-power over the three action steps). For the beta-frequency band, on the other hand, there was a significant main effect of Step ($F(2,54) = 19.54, p < 0.001, \eta^p = 0.42$). [Fig. 2A](#) shows the averaged relative beta-power for the three Steps at Cz, and [Fig. 2B](#)

illustrates the topographic distribution of the effect. To further investigate the main effect, we conducted paired-sample t -tests which showed that relative power was larger for Step1 compared to Step2 ($M = 0.10, SD = 0.16, t(27) = 3.33, p = 0.003, d = 0.61$) and Step3 ($M = 0.17, SD = 0.16, t(27) = 5.71, p < 0.001, d = 1.00$), and larger for Step2 compared to Step3 ($M = 0.07, SD = 0.11, t(27) = 3.30, p < 0.003, d = 0.49$). A decrease of beta-power is seen as a reflection of increased motor system activity ([Perry and Bentin, 2009; Pfurtscheller, 1981; Pineda, 2005](#)) and these results hence suggest that participants showed increased motor system activation for the later compared to the earlier action steps.

3.2.1. Beta frequency power during catch trials

In our design, predictability always increased gradually during video presentation: the first step was least predictable and the last step was most predictable. It could be argued that our findings of stronger beta-attenuation for later action steps described above are therefore not due to an increase in predictability of the action steps, but due to stimulus duration, reflecting a build-up of motor system activation during the observation of a complex action. To assess this potential alternative explanation, we performed an additional analysis of beta-frequency attenuation during the catch trials. In the catch trials, participants were also presented with a complex multi-step actions similar to the actions used in the main experiment (see [Supplementary Fig. 1](#) for an example). Yet for the catch trials, the presented action steps never lead to the conclusion of the overall action goal, and predictability hence did not increase over the course of the action. If our results were due to a build-up of motor system activity during the continuous observation of complex human actions, rather than due to predictability of the different action steps, a build-up of beta-attenuation should also be visible during the catch trials as well.

Catch trial were analyzed following the same procedures as used in the main analysis and a full description of the analysis can be found in the [Supplementary materials](#). Importantly, a repeated measures ANOVA on the relative beta-frequency power showed no effect of Step on beta-power attenuation during the catch trials ($F(2,54) = 2.15, p = 0.127$, see [Supplementary Fig. 1B](#) for a visualization). There was thus

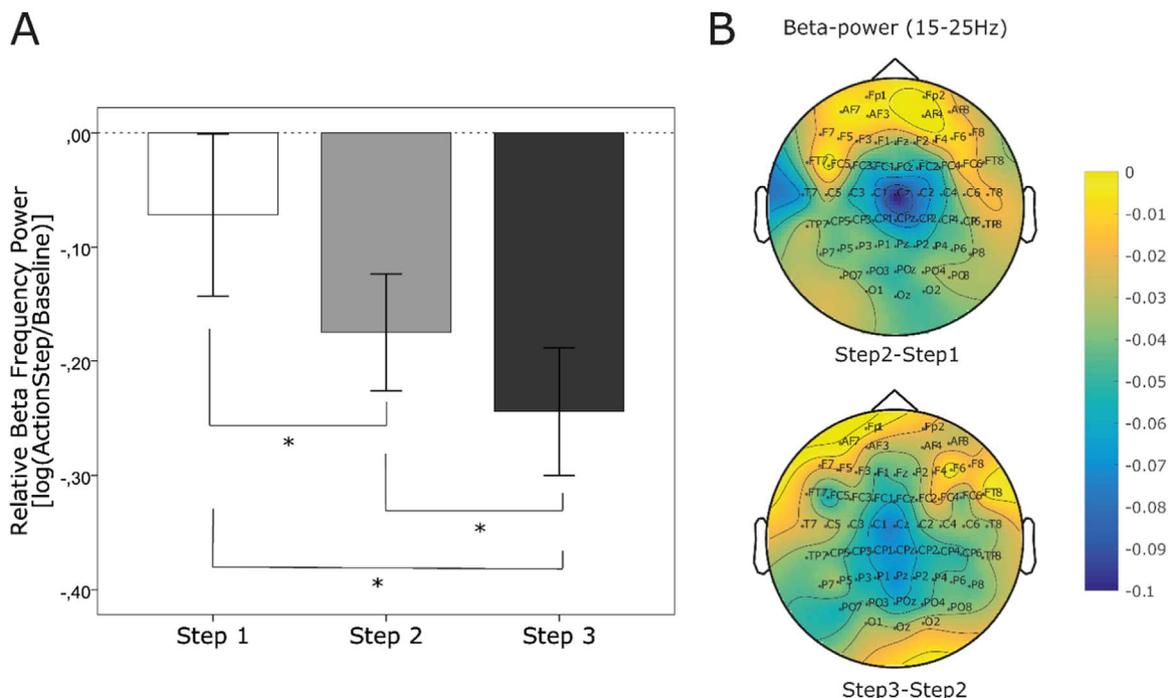


Fig. 2. A) The bar graph showing the relative beta-frequency power over central electrode Cz for the three action steps. Error bars indicate ± 2 SE; significant differences ($p < 0.05$) between the action steps are marked by the asterisk B) Topographic plot of the difference in beta-power for neighboring action steps. Blue colors indicate less power for later compared to earlier action steps.

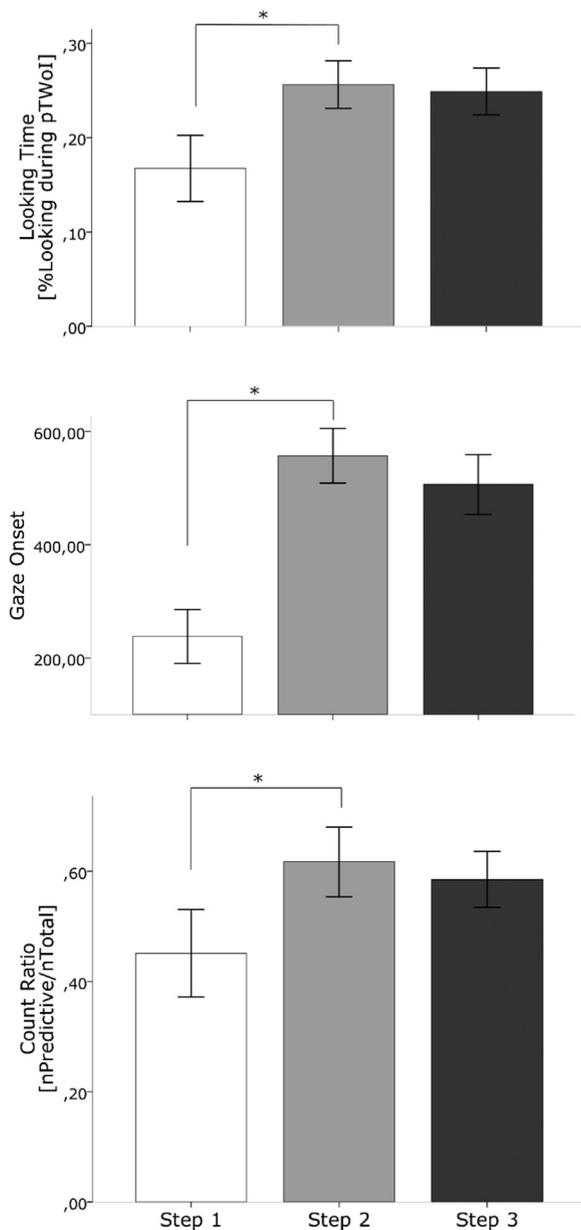


Fig. 3. Eye-tracking results. Error bars \pm 2SE; significant differences ($p < 0.05$) between the action steps are marked by the asterisk.

no gradual decrease of beta-power during the observation of the catch trials which suggests that stimulus duration cannot explain the main findings of stronger beta-attenuation for later, more predictable action steps.

3.3. Eye-tracking results

An overview of the eye-tracking results can be found in Fig. 3. A significant main effect of Step was found for all three dependent measures (Predictive Looking Time: $F(2,42) = 21.45$, $p < 0.001$, $\eta^2 = 0.51$; Predictive Gaze Onset: $F(2,42) = 58.21$, $p < 0.001$, $\eta^2 = 0.74$; Predictive Count Ratio: $F(2,42) = 15.89$, $p < 0.001$, $\eta^2 = 0.43$). To further assess differences between the three Steps, paired-sample t -tests were performed. Results were similar for all three measures, showing a difference between Step1 and Step2 (Predictive Looking Time: $t(21) = -5.90$, $p < 0.001$, $d = -1.20$; Predictive Gaze Onset: $t(21) = -10.82$, $p < 0.001$, $d = -2.83$; Predictive Count Ratio: $t(21) = -4.92$, $p < 0.001$, $d = -0.97$) as well as Step1 and Step3 (Predictive Looking Time: $t(21) = -5.24$, $p < 0.001$, $d = -1.11$; Predictive Gaze Onset:

$t(21) = -8.30$, $p < 0.001$, $d = -2.27$; Predictive Count Ratio: $t(21) = -3.79$, $p = 0.001$, $d = -0.82$). There was, however, no difference between Step2 and Step3 (Predictive Looking Time: $t(21) = 0.51$, $p = 0.616$; Predictive Gaze Onset: $t(21) = 1.51$, $p = 0.147$; Predictive Count Ratio: $t(21) = 1.38$, $p = 0.182$). This indicates that participants showed more, as well as, longer and faster predictions during the last two action steps compared to the first one.

3.4. Correlation analysis

To examine the relationship between predictive motor system activity and predictive eye-movements, we derived the difference in prediction between the action steps for each of our dependent measures and assessed whether eye-tracking and EEG measures were correlated with each other. An overview of all correlation coefficients, test-statistics and correlation plots can be found in Supplementary Table 3 and Supplementary Figs. 3 and 4. We also assessed the correlations between the three different eye-tracking measures which can be found in Supplementary Table 4. Differential beta-power was significantly correlated with Predictive Gaze Onset when contrasting Step 1 and Step 2 ($r = -0.54$, $p = 0.018$, see Fig. 4, upper left panel). Stronger behavioral predictions, indicated by an earlier gaze onset for the later step, were related to a larger decrease in beta-power from Step1 to Step2. Similarly, we also found a marginally significant correlation between Predictive Looking Time and beta-power for the difference score contrasting Step2 and Step3 ($r = -0.41$, $p = 0.083$, see Fig. 4 upper right panel). Again, stronger behavioral predictions, indicated by a longer looking times for the later step, were correlated with a larger decrease in beta-power from Step2 to Step3.

We also found significant correlations between the same two eye-tracking measures and mu-power, although in opposing directions. For the contrast comparing Step 2 and Step 3, mu power – like beta-power – was negatively correlated with Predictive Looking Time ($r = -0.46$, $p = 0.046$, see Fig. 4 lower left panel). For the contrast comparing Step1 and Step2, however, we found a positive relationship between mu-power and Predictive Gaze Onset ($r = 0.46$, $p = 0.048$, see Fig. 4 lower right panel): An earlier gaze onset for the later step was related to a smaller decrease in mu-power from Step1 to Step2.

4. Discussion

Previous research on the role of the motor system in action prediction has primarily focused on simple one-step goal-directed actions (Elsner et al., 2013; Kilner et al., 2004; Koelewijn et al., 2008). The present study investigated the role of the motor system in the integration and prediction of distinct action steps within a multi-step action sequence. Using EEG and eye-tracking, we assessed participants' motor system activation and predictive eye-movements during an action observation task. We found significant attenuation of both mu- and beta-power during action observation compared to baseline. This is in line with previous research, linking attenuation in these frequency ranges to motor system activation (Brinkman et al., 2014; McFarland et al., 2000; Meyer et al., 2015; Perry et al., 2010; Pfurtscheller, 1981; Pineda, 2005; Denis et al., 2016). More importantly, and confirming our hypothesis, we found an increase in motor system activity depending on the action step predictability: Sensorimotor beta-power decreased over the course of the action showing the least attenuation prior to the first (least predictable) action step and most attenuation prior to the last (most predictable) action step. Importantly, no such decrease in beta-power was evident for the catch trials, supporting the interpretation that the observed activity was related to the action's predictability rather than simply being the result of build-up of activation elicited by the observation of a complex multi-step action. Furthermore, our results showed that participants' anticipatory eye-movements were also modulated by predictability, and we found a relationship between neural and behavioral measures: Participants who showed a larger

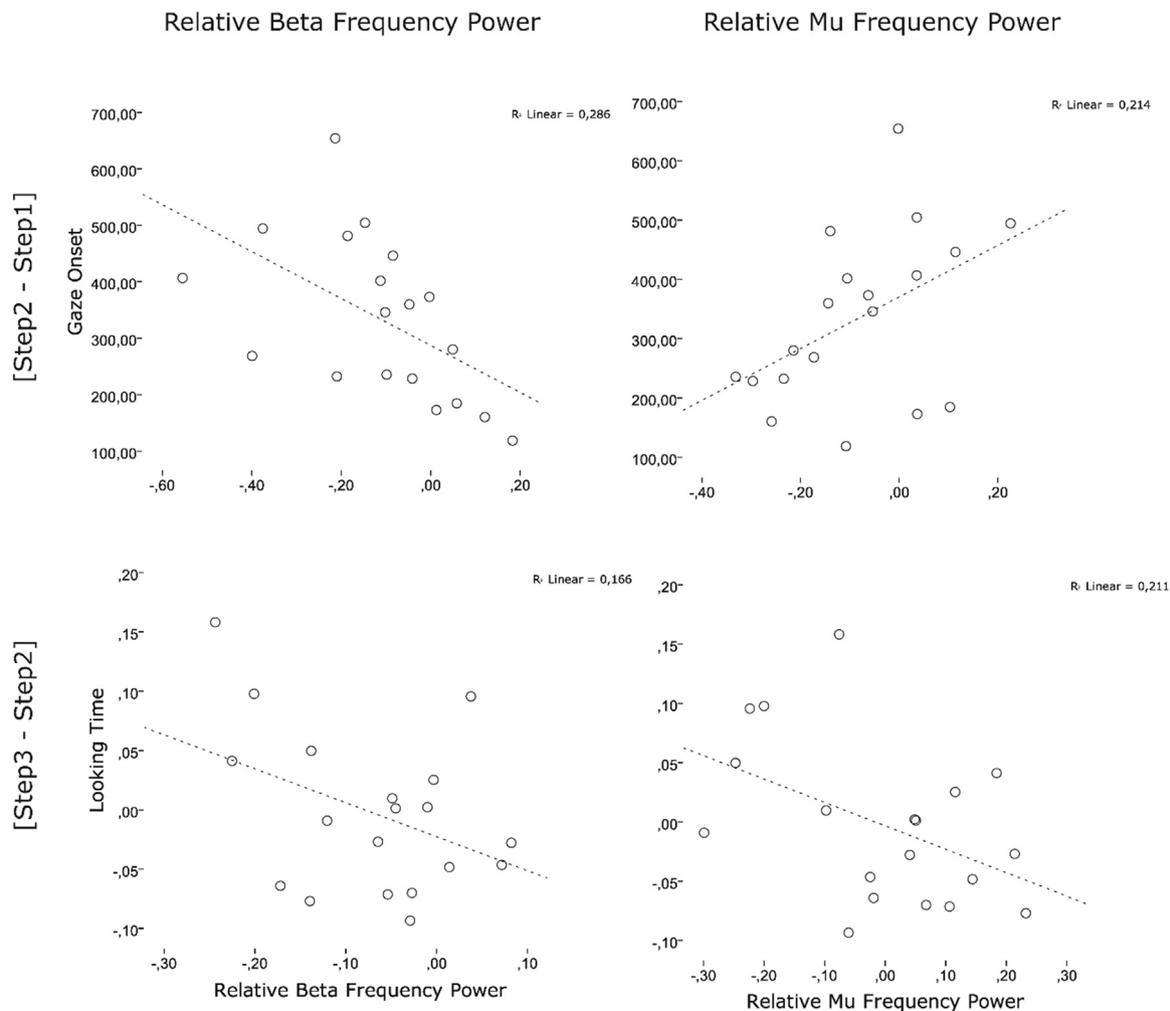


Fig. 4. Scatter plot of the (marginally) significant correlations between the EEG and Eye-tracking data derived from subtracting Step1 from Step2 (upper panel) and Step2 from Step3 (lower panel). The left plots shows the relationship between beta-power and Gaze Onset (upper), and beta-power and Looking Time (lower). The right plots shows the relationship between mu-power and Gaze Onset (upper), and mu-power and Looking Time (lower). Scatter plots of the remaining investigated correlations can be found in supplementary material Figs. 3 and 4.

attenuation of beta-power for later compared to earlier action steps, also showed a larger increase in duration and onset of behavioral anticipations. Although this relationship was not significant for all of the eye-tracking measures we assessed and needs to be interpreted with caution, a link between neural and behavioral markers of prediction is in accordance with previous findings showing that the motor system is involved in the generation of predictive eye-movements (Elsner et al., 2013). Notably, we also found correlations between the eye-tracking measures and mu-attenuation. However, as will be discussed below in more detail, the pattern of the relationship was inconsistent across action steps (see Supplementary Figs. 3 and 4) and one needs to be cautious in interpreting these findings because of the absence of a main effect of Step for the mu-frequency band in our main analysis.

4.1. Predictions in the motor system: the role of sensorimotor oscillations

The results of current study suggest that motor system activation, reflected by attenuation of beta-power, increased based on the predictability of observed action steps. These findings are in line with the suggested role of the motor system in the generation of action predictions (Elsner et al., 2013; Kilner et al., 2007; Prinz, 2006; Schubotz, 2007). Moreover, our findings complement recent fMRI research suggesting that brain regions involved in action perception (i.e. premotor, parietal and occipitotemporal areas, often referred to as the action observation network (AON), see Cross et al., 2012; Cross et al., 2009;

Gazzola and Keysers, 2009; Schubotz, 2007) are modulated by action predictability (Plata Bello et al., 2015; Wurm et al., 2014). Wurm et al. (2014), for instance, assessed the processing of multi-step actions which were either characterized by the presence of an overarching action goal or not (see also Hrkač et al., 2014). Using this paradigm, the researchers investigated, among other things, the effect of goal predictability on brain activation. In the goal-coherent action observation condition, the overall action goal became more predictable towards the end of the action sequence. Wurm et al. (2014) showed that activity in several regions of the AON – in particular in the inferior frontal gyrus and occipitotemporal cortex – decreased as a function of goal predictability. These findings support the notion that the action observation network is modulated by action predictability (see also Plata Bello et al., 2015).

Our study focused on activation of the neural motor system during action observation and aimed to assess whether and in what way neural oscillations associated with the processing of own and other's actions are also modulated by action predictability. Using EEG, we found that attenuation of central sensorimotor beta-power became stronger over the course of the observed actions when the distinct action steps became more predictable. Importantly, beta-attenuation did not differ over time during the observation of catch trials, which displayed similar complex multi-step actions but without the increase in predictability towards the last action step. These results suggest that the observed activity during the experimental trials cannot simply be explained by the continued presentation of a complex action sequence. Rather, the

findings suggest a modulation of motor system activity by action predictability and an involvement of beta-oscillations in the predictive processing of the motor system.

As naturalistic stimuli of everyday action sequences were used, the presented action steps differed in the movement complexity. The action sequence usually started with the actor reaching towards one of the objects, followed by a manipulation of the object, and finally continuing with another reaching action. Performed movements during the middle action step were hence more complex, whereas the first and last action step consisted of simple reaching actions. Differences in movement complexity, however, cannot explain our current results. If movement complexity modulated motor system activation, one would expect to find a peak of activation at Step2 and no differences between Step1 and Step3, rather than an increase of activity over the course of the action. Our study yielded a significant difference between Step1 and Step3 for the eye-tracking measures as well as an overall decrease of beta-band attenuation between all action steps. This supports our interpretation that the current findings reflect a modulation by predictability, rather than reflecting other stimulus features such as movement complexity.

Interestingly, we found a modulation by predictability for the beta-frequency range, but no effect was present for mu-oscillations. Although both oscillations are typically associated with motor system activation (McFarland et al., 2000; Muthukumaraswamy and Johnson, 2004; Perry et al., 2010; Pfurtscheller, 1981), research on mental simulation of goal-directed actions has also suggested that mu- and beta-oscillations serve distinct functions (Brinkman et al., 2014). In addition, neuroimaging studies have reported differences in the origin of the two sensorimotor rhythms (Ritter et al., 2009; Salmelin and Hari, 1994). Two studies that investigated the processing of errors in the motor system have shown that beta-power is modulated by observing erroneous compared to correct actions (Koelewijn et al., 2008; Meyer et al., 2015). One of those studies also assessed mu-power and showed no modulation by action correctness in adults (Meyer et al., 2015). This specificity of beta-power being modulated by erroneous – or unpredicted – events is in agreement with our current findings, suggesting that oscillations in the beta-frequency range may be associated with predictive processing in the motor system. Moreover, a recent study by Tzagarakis et al. (2010) has linked beta-oscillations to response uncertainty, showing that beta-power prior to the execution of a movement was lowest when the movement direction was most predictable. Similarly, Tan et al. (2016) also showed a relationship between post-movement beta-power and model uncertainty which was modulated during a visuomotor adaptation task. Using MEG, van Pelt et al. (2016) studied beta- and gamma-oscillatory in an action observation paradigm in which the probability of kinematic aspects and action outcomes were manipulated, leading to different probabilities for the different kinematic-outcome combinations. The researchers found an increase in beta-band power in the temporoparietal junction along with the kinematics-outcome predictability. Although their study did not focus on motor system activation and utilized a different paradigm, the link between beta-oscillations and predictability is in keeping with our findings.

Sensorimotor mu-oscillations, on the other hand, were attenuated during action observation but did not show a modulation by predictability in the current study. These findings suggest that mu-oscillations may reflect a general non-specific mechanism of motor system activation. This interpretation is in agreement with findings by Meyer et al. (2011) who investigated motor system activation in toddlers during the observation of a joint action partner. The authors reported that activity in the beta-frequency range was related specifically to the timing of the other person's action, while power in the mu-frequency range was persistent throughout the whole observation window that was investigated.

4.2. Motor system activity and predictive eye-movements

In this study, we examined three measures of predictive eye-movements which all showed significant differences between the first and the last two action steps. These findings are consistent with work by Poljac et al. (2014), showing that during the observation of an unfolding action sequence, stronger behavioral predictions can be observed for later, more predictable, action steps. Slight differences between the results of the two studies¹ are likely to be caused by differences in stimulus material as well as the resulting time windows and AOs used in the analysis.

The current study extended the previous findings by examining the neural underpinnings of predictions during action observation as well as the relationship between neural and behavioral markers of predictions. Recent work showed that the motor system is directly involved in the generation of predictive eye-movements (Elsner et al., 2013). In accordance with this, we found a significant correlation between the two measures of prediction: Participants who showed a stronger beta-attenuation from the first to the second action step, also showed a greater increase in Predictive Gaze Onset. Although only marginally significant, we found a similar relationship between beta-attenuation from the second to the third action step and Predictive Looking Time. While these findings support the tight link between motor system activation and behavioral action predictions, it needs to be noted that the remaining correlations between beta-power and predictive eye-movements did not reach significance and the findings thus need to be interpreted with caution. Interestingly, while mu-power was not modulated by predictability, we did find significant correlations between eye-tracking measures and mu-attenuation. However, while the relationship between beta-power and predictive eye-movements was consistent (with more motor activity being related to stronger predictions, see also Supplementary Fig. 3), the relationship between mu-power and predictive eye-movements was inconsistent: A stronger mu-attenuation was associated with weaker predictions for Step1 compared to Step 2, whereas it was associated with stronger predictions for Step2 compared to Step3. Given that we found no main effect of action step in our main analysis, the results of the correlational analysis are difficult to interpret. The rationale of this analysis was to see whether increased neural activity for later action steps was related to increased behavioral predictions. However, for the mu-frequency, we did not find any increased activity for later action steps as the main effect of Step was not significant. This absence of a main effect may have resulted in the observed inconsistent relationship between mu-power and behavioral predictions. Overall, we showed that both mu- and beta-power were related to behavioral predictions, but that only for beta-power there was a consistent relationship with stronger attenuation being related to stronger predictions. These findings are in line with our interpretation of the main analysis, suggesting that beta-oscillations in particular are related to predictions in the motor system.

As participants were performing eye-movements during the task, one could argue that the relationship between the EEG and eye-tracking measures is a mere artifact of eye-movements in the EEG data rather than reflecting a true connection between two distinct measures of action prediction. However, we consider this explanation to be unlikely for multiple reasons: First, ICA was applied to detect and remove components from the EEG data that reflected overt eye-movements. Several studies suggest that ICA is a powerful method to correct for eye-artifacts in the EEG data due to the distinct temporal and spatial activation pattern of the eye-movement components (Jung et al., 1998;

¹ In their action observation paradigm, Poljac et al. (2014) found an identical pattern of results (i.e. significant differences between the first and the last two action steps) for the Predictive Looking Time measure only. For Predictive Gaze Onset and Predictive Count Ratio, on the other hand, they reported a difference between the third and the first two action steps, whereas the present study found a difference between the first and last two steps for all three measures.

Plöchl et al., 2012). Second, eye-movement artifacts in the EEG data have been shown to affect mostly higher frequency ranges such as gamma rather than the lower frequency ranges we investigated (Reva and Aftanas, 2004; Yuval-Greenberg et al., 2008). Third, the topographic plots in Fig. 2b show that the difference between the action steps was densely localized around central electrodes making a contamination by eye movement artifacts unlikely. Finally, additional analyses assessing beta-attenuation during the catch trials suggested that beta-power was not different for the distinct action steps in the catch trials. During the catch trials, one would expect similar eye-movements as the catch trials also contained complex goal-directed multi-step actions. If the reported beta-attenuation was merely reflecting eye-movement artifacts, we would thus expect a similar pattern of activation during the catch trials. We therefore would argue that our main results are not confounded by eye-movement artifacts and that correlation analysis reflects a true link between neural motor system activation and predictive eye-movements (see also Elsner et al., 2013).

In summary, the present study demonstrated that attenuation of beta-power, reflecting activity in the motor system, and behavioral predictions become stronger for more predictable sub-steps within a multi-step action. Our findings are in accordance with recent empirical work suggesting distinct functional roles for the sensorimotor mu- and beta-rhythms (Brinkman et al., 2014; Meyer et al., 2011) and linking beta-oscillations to predictions in the motor system (Palmer et al., 2016b).

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at <http://dx.doi.org/10.1016/j.neuropsychologia.2017.07.009>.

References

- Brinkman, L., Stolk, A., Dijkerman, H.C., de Lange, F.P., Toni, I., 2014. Distinct roles for alpha- and beta-band oscillations during mental simulation of goal-directed actions. *J. Neurosci.: Off. J. Soc. Neurosci.* 34 (44), 14783–14792. <http://dx.doi.org/10.1523/JNEUROSCI.2039-14.2014>.
- Cochin, S., Barthelemy, C., Roux, S., Martineau, J., 1999. Observation and execution of movement: similarities demonstrated by quantified electroencephalography. *Eur. J. Neurosci.* 11 (5), 1839–1842. <http://dx.doi.org/10.1046/j.1460-9568.1999.00598.x>.
- Cross, E.S., Kraemer, D.J.M., Hamilton, A.F.D.C., Kelley, W.M., Grafton, S.T., 2009. Sensitivity of the action observation network to physical and observational learning. *Cereb. Cortex* 19 (2), 315–326. <http://dx.doi.org/10.1093/cercor/bhn083>.
- Cross, E.S., Liepelt, R., Antonia, A.F., Parkinson, J., Ramsey, R., Stadler, W., Prinz, W., 2012. Robotic movement preferentially engages the action observation network. *Hum. Brain Mapp.* 33 (9), 2238–2254. <http://dx.doi.org/10.1002/hbm.21361>.
- Cuevas, K., Cannon, E.N., Yoo, K., Fox, N. a., 2014. The infant EEG mu rhythm: methodological considerations and best practices. *Dev. Rev.* 34 (1), 26–43. <http://dx.doi.org/10.1016/j.dr.2013.12.001>.
- Denis, D., Rowe, R., Williams, A.M., Milne, E., 2016. The role of cortical sensorimotor oscillations in action anticipation. *NeuroImage*. <http://dx.doi.org/10.1016/j.neuroimage.2016.10.022>.
- Elsner, C., Falck-Ytter, T., Gredebäck, G., 2012. Humans anticipate the goal of other people's point-light actions. *Front. Psychol.* 3, 120. <http://dx.doi.org/10.3389/fpsyg.2012.00120>.
- Elsner, C., D'Ausilio, A., Gredebäck, G., Falck-Ytter, T., Fadiga, L., 2013. The motor cortex is causally related to predictive eye movements during action observation. *Neuropsychologia* 51 (3), 488–492. <http://dx.doi.org/10.1016/j.neuropsychologia.2012.12.007>.
- Falck-Ytter, T., Gredebäck, G., von Hofsten, C., 2006. Infants predict other people's action goals. *Nat. Neurosci.* 9 (7), 878–879. <http://dx.doi.org/10.1038/nn1729>.
- Flanagan, J.R., Johansson, R.S., 2003. Action plans used in action observation. *Nature*

- 424 (6950), 769–771. <http://dx.doi.org/10.1038/nature01861>.
- Gazzola, V., Keysers, C., 2009. The observation and execution of actions share motor and somatosensory voxels in all tested subjects: single-subject analyses of unsmoothed fMRI data. *Cereb. Cortex* 19 (6), 1239–1255. <http://dx.doi.org/10.1093/cercor/bhn181>.
- Gredebäck, G., Falck-Ytter, T., 2015. Eye movements during action observation. *Perspect. Cogn. Sci.* 10 (5), 591–598. <http://dx.doi.org/10.1177/1745691615589103>.
- Hari, R., 2006. Action-perception connection and the cortical mu rhythm. *Prog. Brain Res.* 159, 253–260. [http://dx.doi.org/10.1016/S0079-6123\(06\)59017-X](http://dx.doi.org/10.1016/S0079-6123(06)59017-X).
- Hrkač, M., Wurm, M.F., Schubotz, R.I., 2014. Action observers implicitly expect actors to act goal-coherently, even if they do not: an fMRI study. *Hum. Brain Mapp.* 35 (5), 2178–2190. <http://dx.doi.org/10.1002/hbm.22319>.
- Hunnus, S., Bekkering, H., 2010. The early development of object knowledge: a study of infants' visual anticipations during action observation. *Dev. Psychol.* 46 (2), 446–454. <http://dx.doi.org/10.1037/a0016543>.
- Jung, T.-P., Jung, T.-P., Humphries, C., Lee, T., Makeig, S., Mckeown, M.J., Sejnowski, T. J., 1998. Removing Electroencephalographic Artifacts: Comparison Between ICA and PCA. Retrieved from <http://citeseerx.ist.psu.edu/viewdoc/summary?doi=10.1.1.30.1292>.
- Kilner, J.M., Vargas, C., Duval, S., Blakemore, S.-J., Sirigu, A., 2004. Motor activation prior to observation of a predicted movement. *Nat. Neurosci.* 7 (12), 1299–1301. <http://dx.doi.org/10.1038/nn1355>.
- Kilner, J.M., Friston, K.J., Frith, C.D., 2007. Predictive coding: an account of the mirror neuron system. *Cogn. Process.* 8 (3), 159–166. <http://dx.doi.org/10.1007/s10339-007-0170-2>.
- Koelewijn, T., van Schie, H.T., Bekkering, H., Oostenveld, R., Jensen, O., 2008. Motor-cortical beta oscillations are modulated by correctness of observed action. *NeuroImage* 40 (2), 767–775. <http://dx.doi.org/10.1016/j.neuroimage.2007.12.018>.
- Lepage, J.-F., Théoret, H., 2006. EEG evidence for the presence of an action observation-execution matching system in children. *Eur. J. Dev. Psychol.* 23 (9), 2505–2510. <http://dx.doi.org/10.1111/j.1460-9568.2006.04769.x>.
- McFarland, D.J., Miner, L.A., Vaughan, T.M., Wolpaw, J.R., 2000. Mu and beta rhythm topographies during motor imagery and actual movements. *Brain Topogr.* 12 (3). <http://www.ncbi.nlm.nih.gov/pubmed/10791681>.
- Meyer, M., Hunnius, S., van Elk, M., van Ede, F., Bekkering, H., 2011. Joint action modulates motor system involvement during action observation in 3-year-olds. *Exp. Brain Res.* 211 (3–4), 581–592. <http://dx.doi.org/10.1007/s00221-011-2658-3>.
- Meyer, M., Braukmann, R., Stapel, J.C., Bekkering, H., Hunnius, S., 2015. Monitoring others' errors: the role of the motor system in early childhood and adulthood. (n/a–n/a) *Br. J. Dev. Psychol.* <http://dx.doi.org/10.1111/bjdp.12101>.
- Muthukumaraswamy, S.D., Johnson, B.W., 2004. Changes in rolandic mu rhythm during observation of a precision grip. *Psychophysiology* 41 (1), 152–156. <http://dx.doi.org/10.1046/j.1469-8986.2003.00129.x>.
- Oostenveld, R., Fries, P., Maris, E., Schoffelen, J.-M., 2011. FieldTrip: open source software for advanced analysis of MEG, EEG, and invasive electrophysiological data. *Comput. Intell. Neurosci.* 2011, 156869. <http://dx.doi.org/10.1155/2011/156869>.
- Palmer, C., Zapparoli, L., Kilner, J.M., 2016. A new framework to explain sensorimotor beta oscillations. *Trends Cogn. Sci.* 20 (5), 321–323. <http://dx.doi.org/10.1016/j.tics.2016.03.007>.
- Palmer, C.E., Bunday, K.L., Davare, M., Kilner, J.M., 2016. A causal role for primary motor cortex in perception of observed actions. *J. Cogn. Neurosci.* 28 (12), 2021–2029. http://dx.doi.org/10.1162/jocn_a.01015.
- Perry, A., Bentin, S., 2009. Mirror activity in the human brain while observing hand movements: a comparison between EEG desynchronization in the??-range and previous fMRI results. *Brain Res.* 1282, 126–132. <http://dx.doi.org/10.1016/j.brainres.2009.05.059>.
- Perry, A., Bentin, S., Shalev, I., Israel, S., Zefevovsky, F., Bar-On, D., Ebstein, R.P., 2010. Intranasal oxytocin modulates EEG mu/alpha and beta rhythms during perception of biological motion. *Psychoneuroendocrinology* 35 (10), 1446–1453. <http://dx.doi.org/10.1016/j.psyneuen.2010.04.011>.
- Pfurtscheller, G., 1981. Central beta rhythm during sensorimotor activities in man. *Electroencephalogr. Clin. Neurophysiol.* 51 (3), 253–264. [http://dx.doi.org/10.1016/0013-4694\(81\)90139-5](http://dx.doi.org/10.1016/0013-4694(81)90139-5).
- Pineda, J.A., 2005. The functional significance of mu rhythms: translating “seeing” and “hearing” into “doing. *Brain Res. Rev.* 50 (1), 57–68. <http://dx.doi.org/10.1016/j.brainresrev.2005.04.005>.
- Plata Bello, J., Modroño, C., Marcano, F., González-Mora, J.L., 2015. Modulation in the mirror neuron system when action prediction is not satisfied. *Eur. J. Neurosci.* 41 (7), 940–948. <http://dx.doi.org/10.1111/ejn.12850>.
- Plöchl, M., Ossandón, J.P., König, P., 2012. Combining EEG and eye tracking: identification, characterization, and correction of eye movement artifacts in electroencephalographic data. *Front. Hum. Neurosci.* 6, 1–23. <http://dx.doi.org/10.3389/fnhum.2012.00278>.
- Poljac, E., Dahlsätt, K., Bekkering, H., 2014. Shared predictive decision-making mechanisms in action and language. *Lang. Cogn. Process.* 29 (4), 424–434. <http://dx.doi.org/10.1080/01690965.2013.791702>.
- Prinz, W., 2006. What re-enactment earns us. *Cortex* 42 (4), 515–517. [http://dx.doi.org/10.1016/S0010-9452\(08\)70389-7](http://dx.doi.org/10.1016/S0010-9452(08)70389-7).
- Reva, N.V., Aftanas, L.I., 2004. The coincidence between late non-phase-locked gamma synchronization response and saccadic eye movements. *Int. J. Psychophysiol.: Off. J. Int. Organ. Psychophysiol.* 51 (3), 215–222. <http://dx.doi.org/10.1016/j.ijpsycho.2003.09.005>.
- Ritter, P., Moosmann, M., Villringer, A., 2009. Rolandic alpha and beta EEG rhythms' strengths are inversely related to fMRI-BOLD signal in primary somatosensory and motor cortex. *Hum. Brain Mapp.* 30 (4), 1168–1187. <http://dx.doi.org/10.1002/hbm.20585>.

- Rizzolatti, G., Sinigaglia, C., 2016. The mirror mechanism: a basic principle of brain function. *Nat. Rev. Neurosci.* <http://dx.doi.org/10.1038/nrn.2016.135>.
- Salmelin, R., Hari, R., 1994. Spatiotemporal characteristics of sensorimotor neuromagnetic rhythms related to thumb movement. *Neuroscience* 60 (2), 537–550. [http://dx.doi.org/10.1016/0306-4522\(94\)90263-1](http://dx.doi.org/10.1016/0306-4522(94)90263-1).
- Schubotz, R.I., 2007. Prediction of external events with our motor system: towards a new framework. *Trends Cogn. Sci.* 11 (5), 211–218. <http://dx.doi.org/10.1016/j.tics.2007.02.006>.
- Southgate, V., Johnson, M.H., Osborne, T., Csibra, G., 2009. Predictive motor activation during action observation in human infants. *Biol. Lett.* 5, 6.
- Stapel, J.C., Hunnius, S., van Elk, M., Bekkering, H., 2010. Motor activation during observation of unusual versus ordinary actions in infancy. *Soc. Neurosci.* 5 (5–6), 451–460. <http://dx.doi.org/10.1080/17470919.2010.490667>.
- Tan, H., Wade, C., Brown, P., 2016. Post-movement beta activity in sensorimotor cortex indexes confidence in the estimations from internal models. *J. Neurosci.: Off. J. Soc. Neurosci.* 36 (5), 1516–1528. <http://dx.doi.org/10.1523/JNEUROSCI.3204-15.2016>.
- Tzagarakis, C., Ince, N.F., Leuthold, A.C., Pellizzer, G., 2010. Beta-band activity during motor planning reflects response uncertainty. *J. Neurosci.: Off. J. Soc. Neurosci.* 30 (34), 11270–11277. <http://dx.doi.org/10.1523/JNEUROSCI.6026-09.2010>.
- van Pelt, S., Heil, L., Kwisthout, J., Ondobaka, S., van Rooij, I., Bekkering, H., 2016. Beta- and gamma-band activity reflect predictive coding in the processing of causal events. *Social. Cogn. Affect. Neurosci.* 11 (6), 973–980. <http://dx.doi.org/10.1093/scan/nsw017>.
- Wurm, M.F., Hrkać, M., Morikawa, Y., Schubotz, R.I., 2014. Predicting goals in action episodes attenuates BOLD response in inferior frontal and occipitotemporal cortex. *Behav. Brain Res.* 274, 108–117. <http://dx.doi.org/10.1016/j.bbr.2014.07.053>.
- Yuval-Greenberg, S., Tomer, O., Keren, A.S., Nelken, I., Deouell, L.Y., 2008. Transient induced gamma-band response in EEG as a manifestation of miniature saccades. *Neuron* 58 (3), 429–441. <http://dx.doi.org/10.1016/j.neuron.2008.03.027>.