Mu Suppression during Anticipation of Predictable Actions

Performed by Other Agents

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ABSTRACT

The mirror neuron system (MNS) becomes active during action execution and action observation, which is presumably reflected by reductions in mu (8-13 Hz) activity in the electroencephalogram (EEG) over the sensorimotor cortex. Although the existence of this system is generally accepted, its function is still debated. The aim of the current study was to investigate the role of the MNS in anticipating others' actions by examining whether the MNS was activated – indexed by mu power suppression – prior to the onset of observed actions when the onset and type of action could be predicted on the basis of environmental cues. Healthy young adults performed and observed cued grasping and placing actions in a card game, while the predictability of the observed actions was manipulated using a fixed set of rules. All actions were performed in a real-life setting. Significant mu suppression, relative to within-trial baseline activity, was found during both action execution and observation. In addition, significant mu suppression was found prior to the onset of executed actions (preparatory motor activity), and, crucially, also prior to observed actions that were predictable. No anticipatory mu reductions were found prior to unpredictable observed actions. These results suggest top-down modulation of MNS activity by conceptual knowledge. This is the first study to demonstrate mu suppression prior to action onset – possibly reflecting MNS anticipatory activity – by explicitly manipulating predictability in a real-life setting.

Keywords: Action observation, EEG, Mirror neuron system, Mu rhythm, Prediction

INTRODUCTION

For successful social interactions it is essential to quickly interpret the others' actions and select appropriate responses. Furthermore, the ability to quickly predict the onset, type and course of the other's action greatly helps to coordinate joint actions. For example, when shaking hands one needs to anticipate where the other's hand will be in time and space to succeed in this joint action. Moreover, even when not required to respond to others' actions, as when spectators passively observe the unfolding of an action (either live or depicted on film), the ability to anticipate actions greatly helps to understand the actions and to determine intentions. In fact, it is hard to imagine what social actions would look like without this ability to quickly anticipate others' actions: joint actions would be virtually impossible, and most of the time one would be utterly surprised and mystified by the course others' actions take.

Early studies using single cell recordings in animals suggested that action performance and observation rely on a partly shared neural system. In 1992, Di Pellegrino and colleagues reported that specific neurons in the premotor cortex of macaque monkeys become active both during the performance of a motor action and while observing another agent performing the same, or a similar, motor action (Di Pellegrino, Fadiga, Fogassi, Gallese, & Rizzolatti, 1992). A few years later, the term mirror neurons was introduced (Gallese et al., 1996; Rizzolatti et al., 1996) and the interconnected areas of mirror neurons are now commonly referred to as the mirror neuron system (MNS). Subsequently, results from non-invasive electrophysiological and neuroimaging techniques suggested the existence of a MNS in humans (e.g. Buccino et al., 2001; Fadiga, Fogassi, Pavesi, & Rizzolatti, 1995; Grafton, Arbib, Fadiga, & Rizzolatti, 1996; Kilner, Neal, Weiskopf, Friston, & Frith, 2009), which was further supported by a single cell study in humans (Mukamel, Ekstrom, Kaplan, Iacoboni, & Fried, 2010). Two areas in the human brain that have generally been found to show mirror neuron properties are the inferior parietal lobule (IPL) and ventral premotor cortex (vPMC; Brodmann area 44), since these areas consistently become active during action execution and observation (for a review, see Rizzolatti & Sinigaglia, 2010), but other areas are implicated as well (Caspers, Zilles, Laird, & Eickhoff, 2010; Mukamel et al., 2010).

Based on a large collection of studies, it is generally assumed that mirror neurons represent an important part of the information processing stream that links perception and

action. Although the existence of the MNS is rarely disputed, its function remains hotly debated (e.g. Aglioti, Cesari, Romani, & Urgesi, 2008; Csibra, 2008; Hamilton & Grafton, 2008; Heyes, 2010; Iacoboni, 2005; Press, Cook, Blakemore, & Kilner, 2011; Rizzolatti & Sinigaglia, 2010). Action mirroring has been suggested to subserve a number of abilities, including action understanding (Gallese, Fadiga, Fogassi, & Rizzolatti, 1996; Rizzolatti & Fabbri-Destro, 2008), imitation (Iacoboni & Dapretto, 2006; Williams, Whiten, Suddendorf, & Perrett, 2001), empathy (Iacoboni, 2005), language (Arbib, 2005), and social perception (Keuken et al., 2011; Moore, Gorodnitsky, & Pineda, 2012).

One contentious issue regarding the MNS relates to its reactive versus predictive role. Originally it was assumed that the MNS becomes active reactively, in response to bottom-up visual input (e.g. Rizzolatti et al., 1996). This idea was criticised by researchers who assumed that the MNS was activated by top-down cognitive processes involved in, for example, the interpretation of contextual information (e.g. Csibra, 2008). In addition, several models, such as the modular selection and identification for control (HMOSIAC) model (Wolpert, Doya, & Kawato, 2003), predictive coding model (Kilner, Friston, & Frith, 2007), social top-down response modulation (STORM) model (Wang & Hamilton, 2012), and the Hebbian learning model (Keysers & Perrett, 2004), propose that bottom-up and top-down processes are both involved in action mirroring. Although these models vary in many aspects, they have in common that they incorporate a predictive role for the MNS. For example, Kilner, Friston, & Frith (2007) proposed that a predictive coding framework can be applied to the MNS, in which predictions are made about lower-level representations, such as motor kinematics, on the basis of higher-level representations of actions in terms of goals and intentions. These predictions pertain to the specific motor kinematics that would have to be performed to achieve the inferred outcome. The continuous stream of bottom-up visual input is used to verify/correct the predictions.

One method to determine whether the MNS becomes active prior to action observation is to measure the exact onset of MNS activity when observing discrete actions. A single-unit electrophysiological study in macaque monkeys reported that a proportion of mirror neurons started to fire in anticipation of an upcoming action performed by another agent when the monkey knew which action was going to be performed (Maranesi, Livi, Fogassi, Rizzolatti, & Bonini, 2014).

In humans, the electroencephalogram (EEG) is a suitable method to examine the time course of the MNS. Among the few EEG studies that explored MNS activity prior to action observation is a study by Kilner and colleagues (2004), in which participants watched videos of hand grasping actions and performed a button press as action execution condition. The contingent negative variation (CNV), an event-related potential (ERP) related to motor preparation (Leuthold, Sommer, & Ulrich, 2004), was used as an electrophysiological index for MNS activity. Results demonstrated similar ERPs prior to action execution and action observation. Moreover, Kourtis and colleagues (2010, 2013a, 2013b) explored the CNV prior to and during joint actions. These studies again demonstrated similar CNV amplitudes prior to observing and performing an action. Based on these studies, a role for anticipatory motor simulation in the MNS was suggested. However, since the experimental design did not explicitly try to avoid motor preparation from seeping through the action observation, and the CNV is primarily considered a marker for motor preparation, it remains possible that the findings of these studies were affected by motor preparation and did not reflect a purely passive observational anticipatory effect.

A more commonly used EEG index for MNS activity is mu suppression (for reviews, see Pineda, 2005; Fox et al., 2016; see Hobson & Bishop, 2016, for a discussion of its limitations). The activity in the MNS is assumed to be reflected by a reduction in power in the mu rhythm, which is in the alpha band (8-13 Hz in adults) over the sensorimotor cortex. The mu rhythm desynchronises during the execution and observation of actions (Salmelin & Hari, 1994). Altschuler and colleagues (1997) were the first to suggest the link between power reductions in the mu rhythm and MNS activity. This link has now been supported by a wide range of studies, using EEG (e.g. Caetano, Jousmäki, & Hari, 2007; Cochin, Barthelemy, Roux, & Martineau, 1999; Muthukumaraswamy, Johnson, & McNair, 2004; Perry & Bentin, 2009; Press, Cook, Blakemore, & Kilner, 2011; Hobson & Bishop, 2016; for a meta-analysis, see Fox et al., 2016), and magnetoencephalography (MEG; e.g. Hari et al., 1998; Hari & Salmelin, 1997; Salmelin, Forss, Knuutila, & Hari, 1995). Although event-related desynchronizations (ERDs) in the mu rhythm have routinely been recorded during action observation, the exact timing of their onset has only rarely been studied. Caetano and colleagues (2007) examined ERDs in the beta (14-30 Hz) frequency range in a MEG study prior to and during both action execution and observation. They found that observing

others' cued actions generated ERDs around 20 Hz, which started approximately 0.8 s before onset of the action.

So far, anticipatory responses in the mu rhythm to others' actions have been studied mainly in infants. For example, when nine-months-old infants reached for toys after which they saw an actor reach for the toys, mu suppression prior was found prior to action observation (Southgate, Johnson, Osborne, and Csibra, 2009). These findings were replicated in another study by Southgate and Begus (2013). The authors interpreted the results as evidence for top-down input to the MNS enabling an anticipatory function for the MNS. However, these effects have not yet been confirmed in adults, and predictability of the actions had not been manipulated (i.e. all actions were predictable).

The current study aimed to further investigate the functional role of the MNS. Numerous studies have addressed the involvement of the MNS in action understanding (e.g. Cattaneo, Maule, Barchiesi, & Rizzolatti, 2013; Fogassi et al., 2005; Iacoboni et al., 2005; Rizzolatti et al., 1996), but little is known about its contribution to action anticipation, which is the main aim of the present study. We hypothesised that an involvement of the MNS in action anticipation would be reflected by activity in the MNS starting prior to the onset of the observed action, when the onset and type of action was predictable, but that such activity would be absent when onset and type of action were not predictable. To this end, we explored the time course of power in the mu rhythm across the sensorimotor cortex (Fox et al., 2016; but see Hobson & Bishop, 2016, for some cautionary comments). EEG recordings were made during the execution and observation of (un)predictable goal-directed hand actions.

Previous studies investigating the role of the MNS in social cognition used either real-life or video stimuli, though often without strong reasoning why one or the other was selected. Several studies have suggested superiority of real-life over video stimuli in humans with respect to the activation of brain systems (Järveläinen, Schürmann, Avikainen, & Hari, 2001; Ruyschaert, Warreyn, Wiersema, Metin, & Roeyers, 2013; Shimada & Hiraki, 2006). In the current study the actions were presented in a real-life setting as the improved ecological validity might enhance the responses in the mu rhythm and any anticipation effects. In this real-life setting, hand movements to grasp and displace playing cards were performed by either the participant or experimenter in three conditions: 1) action execution, in which the

participant executed hand movements to grasp and place cards, 2) observation of predictable actions, in which the participant anticipated and observed hand actions carried out by the experimenter, and 3) observation of unpredictable actions, in which the participant observed hand actions whose occurrence could not be anticipated. The expectation was that in the action execution condition, as a result of motor preparation, mu suppression would be found in the period before action onset. In the observation of predictable actions condition, mu suppression prior to action onset would support the anticipatory role of the MNS. This would be further supported if in the observation of unpredictable actions condition no such MNS activity would be found prior to action onset, as context information did not indicate whether or not an action was going to be observed. To the best of our knowledge, this study is the first to examine mu suppression before the onset of action observation in adults, where predictability is explicitly manipulated.

METHODS

Participants

Twenty-three volunteers participated in the study (18 women; average age of 22.1 years, SD = 6.7, range 19-45). The group consisted of right-handed typically-developed (under-) graduate students from the Psychology department of the University of Hull. All participants had normal or corrected vision. The undergraduate students received credits towards their degree for participating. The study was approved by the ethics committee of the Psychology department of the University of Hull.

Procedure

After providing oral and written information about the study and obtaining informed consent from the participants, EEG data was recorded during the execution and observation of actions. Depending on the experimental condition, either the participant displaced playing cards, or the experimenter displaced them while the participant observed the actions. Playing cards were chosen as the to-be-manipulated objects, because they require a specific hand grip for picking up (i.e. precision grasp), can easily be incorporated in a game that follows a set of fixed rules (e.g. half are red and half are black), and are well-known. The face cards were removed from the set, since it was important that participants could recognize

the colour of the symbols on the cards quickly, which is more difficult for face cards. The 40 remaining cards were used as objects for goal-directed hand actions. The deck of cards was positioned on top of a tablet PC placed directly in front of the participant or experimenter (depending on the condition) on the table.

The experiment consisted of three conditions, performed across three separate blocks in fixed sequence: Execution, Observation with rule (observing predictable actions), and Observation without rule (observing unpredictable actions). The Execution condition was done first, since previous studies suggested that the performance of actions might enhance motor simulation of observed actions (van Elk et al., 2008; Marshall et al., 2009). Therefore, it was expected that this order would result in stronger effects during action observation compared to the reverse order of conditions. To avoid motor preparation as a confounding factor, action observation and execution conditions were not intermixed, but presented in a block design. Figure 1 depicts a schematic overview of the three conditions. Note that the observed hand actions were performed in the observer's peripersonal space, since previous studies suggested that this leads to stronger motor simulation compared to extrapersonal space (Griffiths & Tipper, 2009, 2012).

Prior to each condition, the participant received specific instructions pertaining the rules applying to that particular condition. The rules were related to the colour of the tablet screen, with a white colour as default, and red, black and blue as signal colours after which the gasping and placing actions were performed. All actions were performed with the right hand. Before and after the action, the right hand of the participant (execution condition) or experimenter (observation conditions) rested on a touchpad next to the tablet. The touchpad was connected to the AD-box of the EEG system, so that the exact timing of the action onset and action ending could be determined.

Execution condition: Participants were instructed to pick up the top card and place it on the discard pile located 20 cm behind the initial deck (further away from the participant; Figure 1), only if the colours of the card and of the signal on the tablet screen were identical (i.e., both red or both black). They had to pick up the card as soon as the tablet colour signal changed back to white. In half of the trials, the colours matched and the participant thus had to perform this action, in the other half of trials the colours did not match and no action was performed (i.e., participant's hand remained rested on the touchpad).

Observation with rule condition: The Execution condition was followed by a 5-minute break, after which the Observation with rule condition began, where the participants observed the experimenter perform the same actions as they performed in the Execution condition. Participants were again instructed about the rule, and were thus able to predict the actions of the experimenter based on a match or mismatch between the colour of the card and colour of the signal.

Observation without rule condition: After again a 5 minute break the Observation without rule condition began. The participant was instructed that the occurrence of the experimenter's action (pick up the top card and displace it) could no longer be predicted on the basis of the colour match/mismatch of top card and tablet signal. In each trial the colour of the tablet became blue, and in half of the trials the cards were picked up by the experimenter in a quasi-random sequence.

An important aspect of the current design is that the Observation with rule and Observation without rule conditions are visually completely identical, which means that any differences in mu power found when comparing these two conditions has to result from the difference in anticipation. There are arguably also no major differences in attentional engagement between the two conditions.

There were 80 trials in each condition (plus two practice trials prior to each condition to ensure the participant had understood the rule), of which 40 were action trials and 40 were non-action trials. Within each condition, the trials were presented in one of two fixed orders, counterbalanced across participants. The orders were fixed to ensure that half of the trials were action trials. The task was relatively simple so that errors in adhering to the rule were negligible. In total, three mistakes were made by either the participant (2) or experimenter (1) and these trials were removed from the data set.

Each trial lasted about 13 seconds: 1 second yellow tablet screen to indicate the onset of a trial, 2 seconds signal tablet screen, and 9 to 11 seconds white tablet screen during which actions did or did not take place. This last period varied in duration to minimise time-locked effects during the clips. Actions started approximately 1 second after cessation of the tablet signal and lasted for approximately 3 seconds, resulting in at least 5 seconds rest between the trials. All actions in the observation conditions were executed by one and the same well-trained experimenter (MAK). Therefore, the timings in these conditions were relatively

consistent, while in the Execution condition the timing had more variability, as these actions were performed by participants. Each block lasted about 17 minutes, with a 5-minute break in between blocks, so that the total EEG experiment lasted approximately one hour.

Figure 1 - The three real-life conditions. The set-up of the Execution condition (top panel), Observation with rule condition (middle panel) and Observation without rule condition (bottom panel) are displayed. For each condition an action trial is shown, with the (approximate) timings of the phases.

EEG Recording

EEG was recorded from 64 scalp locations according to the International 10-20 EEG System using Ag–AgCl-tipped electrodes (sampling rate: 512 Hz). Raw EEG recordings were made with the ActiveTwo system (BioSemi, Amsterdam, The Netherlands) relative to the common mode sense (CMS). By physically integrating the first amplifier stage with a sintered Ag–AgCl electrode, extremely low-noise recordings free of interference were achieved. The ground consisted of the active CMS and passive driven right leg (DRL) electrodes that form a feedback loop driving the subject's average potential as close as possible to the analog-to-digital converter reference voltage in the A/D-box (i.e., the amplifier “zero”). The CMS electrode was located in between P1, PO3, and POz and the DRL electrode was placed in between P2, POz, and PO4. A touchpad was connected to the Ergo input in the AD-box for isolated auxiliary signals. The touchpad consisted of a pressure-activated membrane switch, which elicited a 4 V signal when a hand was placed on it; if not, no voltage was elicited (Pal Pad, Adaptation, Inc., Sioux Falls, United States).

EEG Analysis

BrainVision Analyzer 2.1.1 (Brain Products GmbH, Gilching, Germany) was used to analyse the raw data files offline. First the data was re-referenced to an average reference. The 8-13 Hz frequency band was extracted with a Butterworth Zero Phase bandpass filter (48 dB/oct). Markers were automatically placed on the data file for the on- and offset of the actions, based on the signal from the touchpad; a visual inspection was done to remove incorrect markers. Next the data was segmented from 5 seconds before till 5 seconds after the onset of actions. Segments with artifacts were removed ($< -50 \mu\text{V}$; $> 50 \mu\text{V}$) and the data was rectified. The data was then baseline corrected with as baseline period the one-second epoch beginning 5 seconds before the onset of an action.

After averaging the data of all the action trials per block, power in squared microvolt (μV^2) was exported for a cluster of 9 electrodes at the left hemisphere (C5, C3, C1, CP5, CP3, CP1, P5, P3, and P1) and a cluster of 9 electrodes at the right hemisphere (C2, C4, C6, P2, P4, CP6, P2, P4, and P6). These electrodes (see Figure 2) were selected to cover the cortical areas involved in sensorimotor representations of hand and arm actions (Babiloni et al., 2002). Similar clusters were analysed in a number of previous studies in which hand/arm actions

were presented (e.g. Avanzini et al., 2012; Bernier, Dawson, Webb, & Murias, 2007; Coll, Bird, Catmur, & Press, 2015; Kourtis et al., 2013; Muthukumaraswamy et al., 2004; Southgate, Johnson, Karoui, & Csibra, 2010; Southgate et al., 2009; Southgate & Begus, 2013).

The power in the mu rhythm was extracted using temporal spectral evolution (TSE; Salmelin & Hari, 1994), which transforms raw data into power in a selected frequency band without inducing changes in the time-domain. This method has been used successfully by other studies that investigated mu suppression (Babiloni et al., 2002; Caetano et al., 2007; Hari et al., 1998; Kourtis et al., 2013b; Ohara et al., 2000; Salmelin, Forss, Knuutila & Hari, 1995; Salmelin, Hämäläinen, Kajola, & Hari, 1995; Salmelin & Hari, 1994). It is especially useful for analysing the time course of power in a certain frequency band, as the temporal resolution of the data remains at sampling rate.

Data reduction and statistical analysis

The condition in which unpredictable actions (i.e., Observation without rule) were presented was introduced after the first six participants were tested. In addition, one of the participants was not able to complete this condition, which means there were 23 participants in the first two conditions (i.e., Execution and Observation with rule) and 16 participants that completed all three conditions. Although there is quite some variability in the extent of mu rhythm present across individuals, and, according to Hobson & Bishop (2016), between 16 and 21% of neurotypical participants do not show any mu suppression in response to action observation, we did not seek to exclude participants for these reasons and examined the grand average of all participants. We thus employed a quite conservative method to find evidence of mu suppression.

For the statistical analysis, first mu suppression in the three conditions were compared in an ANOVA with Condition (3 levels: Execution, Observation with rule, and Observation without rule), Time (5 levels: 5 seconds, from 2 seconds before action onset till 3 seconds after action onset), and Hemisphere (2 levels: LH and RH) as within-subject factors. Greenhouse-Geisser corrections were applied whenever Mauchly's test of sphericity was significant. Next, the magnitude of mu suppression prior to, and during, the execution and observation of actions was compared with the level of power in the, within-trial, baseline phase, using one-sample t-tests.

RESULTS

The selected electrodes in the 10/20 system and power reductions in the mu rhythm during action execution are displayed in Figure 2. The observed overlap is a strong indication that these electrode clusters record activity in the sensorimotor system related to hand/arm actions.

Figure 2 - Power reduction during action execution. Power reductions (blue colour) during the Execution condition (Action phase; 0 - 3 s). The a priori selected electrodes consisted of two clusters of nine electrodes around CP3 and CP4, respectively (labelled and filled circles).

Figure. 3 - Time course of power reductions. The top graph depicts power in the mu rhythm averaged over the 9-electrode cluster of the left hemisphere (LH), for each the three conditions: Execution, Observation with rule, and Observation without rule. The bottom graph displays the same information for the right hemisphere cluster (RH). The onset of both executed and observed actions was at time 0. The Delay phase, of around 1 second, is the period in between the Signal phase and the Action phase.

Effect of action predictability

The 3 (Condition) $\times$ 5 (Time) $\times$ 2 (Hemisphere) ANOVA, which was performed to examine any differences between conditions, demonstrated that the main effects of Condition, $F(1.31, 19.61) = 3.23$, $p = .08$, $\eta_p^2 = .18$, and Hemisphere, $F(1, 15) = 2.33$, $p = .15$, $\eta_p^2 = .13$, were not significant. The main effect of Time was significant, $F(1.28, 19.15) = 6.23$, $p = .02$, $\eta_p^2 = .29$, as well as the two-way interaction effect between Time and Condition, $F(2.76, 41.45) = 5.05$, $p = .005$, $\eta_p^2 = .25$. In addition, the three-way interaction effect between Time, Condition, and Hemisphere was significant, $F(1.69, 25.35) = 5.49$, $p = .01$, $\eta_p^2 = .27$. Figure 3 displays the time course of the averaged power reduction for the two electrode clusters for each of the three conditions (for the time course of power in the alpha rhythm for all electrodes over the central, parietal and occipital electrodes, see supplementary figure S1).

Next, 2 (Hemisphere) $\times$ 3 (Condition) ANOVAs were performed for each second, of which the two seconds prior to the onset of the action potentially contain anticipation effects. In the epoch from two till one second before action onset, a significant main effect of Condition was observed, $F(1.36, 20.41) = 9.20$, $p = .004$, $\eta_p^2 = .38$. The three conditions all differed significantly from each other with larger power reductions in the Execution condition ($M = -.27$, $SD = .25$) compared to the Observation with rule condition ($M = -.17$, $SD = .14$), $t(15) = -2.28$, $p = .04$, $d_z = -.57$, and compared to the Observation without rule condition ($M = -.02$, $SD = .13$), $t(15) = -3.29$, $p = .005$, $d_z = -.82$. Crucially, mu power reductions in the Observation with rule condition were larger than in the Observation without rule condition, $t(15) = -2.93$, $p = .01$, $d_z = .73$. Furthermore, there was a significant interaction effect between Hemisphere and Condition, $F(2, 30) = 3.52$, $p = .04$, $\eta_p^2 = .19$.

Two one-way ANOVAs indicated a significant main effect of Condition for both the left, $F(1.27, 19.04) = 9.91$, $p = .003$, $\eta_p^2 = .40$, and right hemisphere cluster, $F(2, 30) = 7.01$, $p = .003$, $\eta_p^2 = .32$. In the left hemisphere (LH), there were significant differences in power between all three conditions; crucially the power reduction in the Observation without rule condition ($M = -.01$, $SD = .15$) was significantly smaller than in the Observation with rule condition ($M = -.17$, $SD = .15$), $t(15) = -2.79$, $p = .01$, $d_z = -.73$. Similarly, power in the right hemisphere (RH) was less strongly reduced in the Observation without rule condition ($M = -.03$, $SD = .11$) compared to the Observation with rule condition ($M = -.17$, $SD = .14$), $t(15) = -2.92$, $p = .01$, $d_z = -.70$. Thus, at both hemispheres power was more strongly reduced prior to

the observation of predictable actions compared to unpredictable actions. The difference between the two hemispheres was that in the LH stronger power reductions were recorded in the Execution condition than in the Observation with rule condition, $t(15) = -2.86$, $p = .01$, $d_z = -.72$, while these two conditions did not significantly differ in the RH, $t(15) = -1.32$, $p = .21$, $d_z = -.33$.

For the one second interval directly preceding action onset again a significant main effect of Condition was found, $F(1.47, 22.10) = 8.36$, $p = .004$, $\eta_p^2 = .36$. Stronger power reductions were again recorded in the Observation with rule condition ($M = -.16$, $SD = .15$), than in the Observation without rule condition ($M = -.01$, $SD = .13$), $t(15) = -2.87$, $p = .01$, $d_z = -.72$. The Execution condition ($M = -.29$, $SD = .27$) showed more power reduction than the Observation without rule condition, $t(15) = -3.28$, $p = .005$, $d_z = -.82$, but did not significantly differ from the Observation with rule condition, $t(15) = -2.09$, $p = .054$, $d_z = -.52$. The Hemisphere by Condition interaction was non-significant, $F(2, 30) = 2.14$, $p = .14$, $\eta_p^2 = .13$.

In the three seconds after action onset (the action epoch), the conditions did not differ in recorded power. In the first second after action onset, the main effect of Condition, $F(1.22, 18.29) = 1.89$, $p = .19$, $\eta_p^2 = .11$, and of Hemisphere, $F(1, 15) = 2.98$, $p = .11$, $\eta_p^2 = .17$, were not significant, nor was the interaction effect, $F(1.33, 19.98) = 2.24$, $p = .15$, $\eta_p^2 = .13$. Similar results were found for the 2nd second (main effect of Condition: $F(1.26, 18.92) = .41$, $p = .58$, $\eta_p^2 = .03$) and 3rd second after action onset (main effect of Condition: $F(1.39, 20.91) = 1.13$, $p = .32$, $\eta_p^2 = .07$).

In sum, marked differences between the three conditions were found, but they were exclusively in the 2 s interval *prior* to action onset, with, crucially, stronger mu suppression in the Observation with rule condition compared to the Observation without rule condition.

Level of mu suppression

In a further analysis, the level of mu suppression prior to, and during, the execution and observation of actions was compared to the level of power in the Baseline epoch, i.e., the 1-second interval starting 5 s before action onset and approximately starting 2 s before onset of the signal epoch (see Table 1 for power reductions). Since a within-trial baseline correction was applied, a negative value would indicate suppression of power in the mu rhythm and a positive value an enhancement (i.e., synchronization). To reduce the number of tests, we

only examined one epoch of 1 second directly prior to action onset (Anticipation epoch/Delay epoch), in between the disappearance of the colour signal and action onset) and one epoch of three seconds directly after action onset (Action epoch; the actions lasted approximately 3 seconds).

Anticipation epoch: One-sample t-tests (test value set to 0) for power reduction between the three conditions and the two electrode clusters were performed (Bonferroni corrections were applied, resulting in an alpha level of significant value of .008). Power in the Delay epoch was significantly reduced compared to the baseline in the Execution condition, LH: $t(22) = -4.37, p < .001, d = -.91$; RH: $t(22) = -4.62, p < .001, d = -.96$. Power reductions in the Observation with rule condition were also significantly reduced, LH: $t(22) = -3.84, p = .001, d = -.80$; RH: $t(22) = -3.87, p = .001, d = -.81$. However, power reductions in the Observation without rule condition did not differ from baseline, LH: $t(15) = .24, p = .82, d = .06$; RH: $t(15) = -1.00, p = .33, d = -.25$.

Action epoch: During the execution of actions, power was significantly reduced for the LH cluster, $t(22) = -3.21, p = .004, d = -.67$, and the RH cluster, $t(22) = -3.35, p = .003, d = -.70$. Similar results were found for the Observation with rule condition, LH: $t(22) = -4.15, p < .001, d = -.87$; RH: $t(22) = -4.25, p < .001, d = -.89$, and for the Observation without rule condition, LH: $t(15) = -4.91, p < .001, d = -1.23$; RH: $t(15) = -4.76, p = .001, d = -1.19$.

In sum, significant mu suppression was found in both the Anticipation and Action epochs of the Execution and Observation with rule conditions, while in the Observation without rule condition mu suppression was only found in the Action epoch and not in the Anticipation epoch.

It is noteworthy to mention that the values of power reduction were quite variable across participants (i.e. relatively large standard deviations). In the Action epoch of the Execution condition, 3 of the 23 participants (approximately 13 percent) showed either no mu suppression or even a synchronization effect. During action observation, 4 participants (approximately 17 percent) did not show mu suppression. These were not the same participants as in the Execution condition. Still, the power reductions were highly significant and a clear desynchronization effect was observed in most participants.

Table 1. Power reductions in the mu rhythm prior to and during action execution and observation.
The average power reduction (and standard deviation) in the 8-13 Hz frequency band during the Anticipation (1 second before action onset) and Action phases (3 seconds after action onset). Data is shown for the separate electrode clusters of the left and right hemisphere and for the average of the two clusters.

Hemisphere	Condition	N	Anticipation	Action
LH	Execution	23	-.24 (.27)**	-.22 (.33)**
	Observation with rule	23	-.12 (.15)**	-.21 (.24)**
	Observation without rule	16	-.01 (.15)	-.24 (.19)**
RH	Execution	23	-.22 (.23)**	-.33 (.47)**
	Observation with rule	23	-.12 (.15)**	-.22 (.25)**
	Observation without rule	16	-.03 (.12)	-.25 (.21)**
Mean	Execution	23	-.23 (.24)**	-.28 (.39)**
	Observation with rule	23	-.12 (.14)**	-.22 (.24)**
	Observation without rule	16	-.01 (.13)	-.24 (.20)**

* $p < .05$, ** $p < .01$

DISCUSSION

The main aim of the present study was to determine whether the MNS becomes activated prior to the onset of predictable versus unpredictable observed actions. First of all, the results showed that the time course of mu suppression was similar when performing or observing an action, both leading to clear power reductions in the mu rhythm, suggesting activation of the MNS. As expected, the mu rhythm was suppressed prior to the execution of actions, indicating action preparation (e.g. Kutas & Donchin, 1980). Although other EEG components have been used as markers for motor preparation, most notably the CNV and the lateralized readiness potential (LRP; Leuthold et al., 2004), here we demonstrated effects of motor preparation in the mu rhythm (corroborating similar findings by Caetano et al., 2007; Feige, Kristeva-Feige, Rossi, Pizzella, & Rossini, 1996; Nagamine, Kajola, Salmelin, Shibasaki, & Hari, 1996; Ohara et al., 2000; Salmelin, Forss, Knuutila, & Hari, 1995). However, the most important finding was that when the observed action was predictable, mu suppression

started about 1.5s prior to the onset of the action, presumably reflecting an anticipation effect. No such mu suppression was observed for unpredictable actions.

The anticipation effect for predictable actions suggests top-down regulation of MNS activity by contextual information (i.e. knowledge about whether or not a particular action would be performed). Top-down input to the MNS forms an integral part of theoretical models, such as the predictive coding model (Kilner et al., 2007). Our findings corroborate previous studies that eluded to an anticipatory role for the MNS using different methodologies (Kilner et al., 2004; Kourtis et al., 2013; Maranesi et al., 2014; Southgate et al., 2009; Southgate & Begus, 2013). However, this is the first study to demonstrate a profound mu power modulation during action anticipation when predictability is explicitly manipulated. Wang and Hamilton (2012) suggested top-down modulation of mimicry in social interactions originating in the medial prefrontal cortex (mPFC), but generally the neural pathways underpinning the top-down influence on the MNS are much less well understood than the bottom-up pathways and require further investigation.

MNS activity was historically observed *during* observation of ongoing actions (Gallese et al., 1996; Rizzolatti et al., 1996), with which it was thought to passively resonate (motor simulation), and was often conceptualized as subserving action understanding (Rizzolatti & Craighero, 2004) and imitation (Iacoboni et al., 1999). Recently though, a more *active* role for the MNS in setting up an anticipatory model of another person's action has been suggested, endowing the brain with the ability to predict/anticipate the other's action ahead of its realization (e.g. Kilner et al., 2004, 2007; Cattaneo et al., 2007). The basic idea is that motor 'resonance', which by definition lags behind the real-time events, is not sufficient to keep up with the pace of social interactions, and that an ability to quickly *anticipate* or *predict* other's actions on the basis of contextual cues is required (Hudson, Liu & Jellema, 2009; Hudson, Burnett & Jellema, 2012). This ability is crucial in social interactions, since it, for instance, enables joint actions (Csibra, 2008; Sebanz & Knoblich, 2009). Else, one would basically continuously lag behind.

A recent single cell study in the macaque monkey provided particularly compelling support for an anticipatory MNS role (Maranesi et al., 2014). This study revealed that a subset of mirror neurons become active prior ($\approx 0.5s$) to the onset of the observed action, but only when the monkey could predict the type and onset of the action on the basis of

contextual cues. One reason such responses have not been seen before, in single cell studies nor in human imaging studies, may be that hitherto testing was typically done in contexts where the predictability was not explicitly manipulated. It should be noted that in the present study the contextual cue was an artificial signal, but in daily life a multitude of contextual cues consists, for example in the form of sub-actions signaling the onset of subsequent sub-actions, as intentional actions typically consist of a smooth sequence of distinct consecutive sub-actions.

An anticipatory role for the MNS ties in with the view that the MNS is primarily involved in the automatic, involuntary, “from within”, understanding of other’s behaviour and emotions (Rizzolatti & Sinigaglia, 2010). This kind of action understanding does not require any deliberate, effortful reasoning processes, but rather happens effortless, and has sometimes been referred to as low-level mindreading (Goldman, 2006). It would particularly suit social interactions, as their pace normally does not allow for any time-consuming deliberate thinking processes (i.e. high-level mindreading). This is not to say that this low-level action understanding does not require the observer to have a Theory-of-Mind (ToM), it most certainly does (Carruthers, 2009; Lavelle, 2012), and can serve to initiate motor simulation as was found in the current study. On the other hand, it has also been argued that an immediate action interpretation can also be derived on the basis of purely perceptual systems without MNS involvement (Vannuscorps & Caramazza, 2016).

Although mu suppression has been assumed to be a reliable measure for MNS activity by many researchers (for a meta-analysis see Fox et al., 2016), critics argued that mu suppression during action observation is small and variable (e.g. Hobson & Bishop, 2016). In the study by Hobson and Bishop (2016), 16-21% of participants showed no mu suppression during action observation. In the present study, 13% and 17% did not show mu suppression during action execution and observation, respectively. We did not exclude these participants, which, if anything, led to an underestimation of effects. The majority of participants did, however, demonstrate profound mu suppression during both action execution and observation, and in two of the three conditions also prior to the onset of actions.

Hobson and Bishop (2016) also cautioned that mu suppression may be confounded by visual information processing. However, it is unlikely that the power reductions in the mu rhythm reported in the present study were mediated by visual processing. Crucially, mu

suppression in response to the observation of predictable actions differed significantly from that to unpredictable actions, while these two observation conditions were visually fully identical. This is an important feature of the current paradigm, which specifically allows to exclude the possibility that differences in visual processing can explain differences in mu reductions. Another indication that the effects were related to the mu rhythm rather than the posterior alpha rhythm - which is a profound oscillation during wakeful rest and is reduced in power by visual input (Berger, 1929) - is the localization of the modulations over sensorimotor cortex, and the gradual decline towards occipital locations (see supplementary figure S1 for an overview of power in the alpha frequency recorded from 29 electrodes).

Another confounding factor that has been suggested to affect mu suppression is attentional engagement (Dujardin et al., 1993; Perry & Bentin, 2010; Hobson & Bishop, 2016). An increase in attentional engagement is known to increase alpha suppression and something similar might happen for the mu rhythm. However, this is an unlikely explanation as the unpredictable actions are, if anything, more likely to attract attention due to the uncertainty about whether or not the actor will pick up the card, whereas in that condition no mu suppression prior to action onset was found. Moreover, attentional modulation is not confined to sensorimotor areas (Dujardin et al., 1993), while the differences in mu suppression were confined to sensorimotor areas.

All actions were observed in a real-life situation, which improved their ecological validity. It is, however, debatable to what extent the observed actions were socially relevant. The actions performed by the agents were private actions and no other confederate was present nor did the agent interact with the observer. Including a confederate could enable interactive actions (e.g. giving and receiving cards). Kourtis and colleagues (2013) did examine action observation in a triadic situation, but a difficulty in these designs is the dissociation between action simulation and motor preparation.

In conclusion, predictability of upcoming actions resulted in activation of the MNS prior to action onset. The findings suggested that the input of the MNS partially consists of predictions about upcoming actions based on knowledge and context information. The present study provided the first evidence of top-down modulation by action predictability in the human MNS using mu rhythm suppression as an index for MNS activity, supporting the claim that the MNS is involved in action anticipation.

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Supplementary figure

Figure S1 - Overview of recorded power in the alpha frequency band. Each graph represents the grand average of power in the 8-13 Hz frequency band during the three conditions for a specific electrode. In total, 29 electrodes are depicted with power (in microvolt; range from 0.3 to -0.6 μV) on the vertical axis and the time from 5 seconds before till 5 seconds after action onset, thus 10 seconds in total, on the horizontal axis (units 0.5s). The vertical green gridline reflects action onset and the grey gridlines indicate the approximate onset of the signal, offset of the signal (onset of delay) and onset of the rest epoch, respectively.