Modulation of motor cortex activity when observing rewarding and punishing actions

Elliot Clayton Brown [1,2]*, Jan Roelf Wiersema[3], Gilles Pourtois[3], Martin Brüne[1,2]

[1] Research Department of Cognitive Neuropsychiatry, LWL University Hospital Bochum, Alexandrinenstrasse 1-3, 44791 Bochum, Germany

[2] International Graduate School of Neuroscience (IGSN), Ruhr University Bochum, Ruhr University Bochum, FNO 01/114 Universitätsstrasse 150, 44801 Bochum, Germany

[3] Department of Experimental Clinical and Health Psychology, Ghent University, Henri Dunantlaan 2, 9000 Gent, Belgium

* Corresponding author: elliot.c.brown@gmail.com
Research Department of Cognitive Neuropsychiatry
LWL University Hospital Bochum
Alexandrinenstrasse 1-3
44791 Bochum, Germany
Tel: +49 234 5077 0

Abstract:

Interpreting others' actions is essential for understanding the intentions and goals in social interactions. Activity in the motor cortex is evoked when we see another person performing actions, which can also be influenced by the intentions and context of the observed action. No study has directly explored the influence of reward and punishment on motor cortex activity when observing others' actions, which is likely to have substantial relevance in different social contexts. In this experiment, EEG was recorded while participants watched movie clips of a person performing actions that led to a monetary reward, loss or no change for the observer. Using the EEG mu rhythm as an index of motor resonance, our results demonstrate that observation of rewarding actions produce significantly greater motor cortex activity than punishing or neutral actions, with punishing actions producing greater activity than neutral ones. In addition, the dynamic change in the mu rhythm over sensorimotor cortex is modulated by reward and punishment, with punishing actions producing a prolonged suppression. These findings demonstrate that the associated reward value of an observed action may be crucial in determining the strength of the representation of the action in the observer's brain. Consequently, reward and punishment is likely to drive observational learning through changes in the action observation network, and may also influence how we interpret, understand, engage in and empathize with others' actions in social interaction.

Keywords: Action observation, reward, punishment, observational learning, mirror neurons

1. Introduction

A fundamental skill required for successful social interaction and social learning is the ability to accurately understand the meaning and intentions of others' behaviour. Albert Bandura's Bobo doll experiments demonstrated that children adopt social behaviours through observation. He showed that children were more likely to imitate others' aggressive behaviour if it was subsequently rewarded, and conversely, were more deterred from imitating the observed behaviour if it was associated with punishment (Bandura, 1977). His highly influential social learning theory proposed that behaviour is shaped during childhood development through positive or negative reinforcement of previously learned imitative actions. The reinforcers of observational learning are determined by the associations made between specific action contents, and the corresponding reward or punishment values. More recently, neuroscientific work has lent support to this assumption. The discovery of an apparently functionally-specific group of "mirror" neurons that become activated when performing goal-directed actions, but also fire when observing others perform similar actions, has fuelled simulation theories of social interaction. Simulation theories such as the direct-matching hypothesis (Rizzolatti et al., 2001), the shared-manifold hypothesis (Gallese, 2003) and the shared circuits hypothesis (Keysers & Gazzola, 2006) generally propose that observed actions are translated, or mirrored, onto the observer's motor cortex, and this simulated motor activity is in turn associated with imitation and consequently social learning. Another main premise of these models is that the simulated, or shared, motor activity seen in the observers' brain while observing others' actions is responsible for the interpretation of others' goals (Blakemore & Frith, 2005). Motor-related shared neural representations during action observation, also referred to as motor resonance, have been thought to form the neural basis of higher level social cognition, including perspective-taking, theory of mind and empathy (Mitchell, 2009).

The original work on mirror neurons was limited to neural recordings performed in non-human primates (Gallese et al., 1996; Rizzolatti et al., 1996), although Mukamel et al. (2010) used single-cell recordings to provide evidence for the existence of mirror neurons in humans. There are also now numerous functional neuroimaging studies that have shown the selective involvement of a frontoparietal network during action observation, including primary motor and premotor cortices, which could be homologous to a mirror neuron system in humans (Gallese, et al., 2004). In EEG, the mu rhythm is an oscillatory activity in the alpha frequency band (8-13Hz) that is specifically associated with motor actions, and is thought to reflect event-related desynchronisation of sensorimotor cortex (Hari, 2006).The suppression of the mu rhythm over sensorimotor areas can be evoked by both the execution and observation of goal-directed actions (Hari, 2006), and therefore it seems to provide a reliable electrophysiological correlate of mirror neuron related activity (Oberman et al., 2005; 2012). Consistent with this assumption, in a previous study that simultaneously recorded EEG and fMRI, the authors found a tight correlation between activity in the proposed human mirror neuron system and the EEG mu suppression during action execution and observation (Arnstein et al., 2011). Moreover, a MEG study from Kilner et al. (2006) found that the mu rhythm can also be modulated by the social relevance of the observed action, and particularly by the relationship between the observer and the performer. Mu rhythm suppression has been found to correlate with measures of empathy, and particularly on the dimensions of perspective-taking and personal distress (Woodruff et al., 2011a, 2011b). Other studies have shown that the perspective from which the action is viewed, can influence motor resonance (Libby et al., 2009), with actions seen from a 1st-person perspective leading to greater action identification. This is thought to be due to the reason that actions seen from an egocentric 1st-person, as opposed to an allocentric 3rd-person perspective, may be easier to translate onto the motor cortex of the observer (Jeannerod & Anquetil, 2008). Hence, accumulating evidence shows that activity in the observer’s motor cortex can be modulated by a variety of social contexts and factors. In this framework, it remains to be established as to whether the perceived reward or punishment value of the observed action is also able to trigger differential motor resonance effects or not, as reflected by systematic changes in the power of the mu suppression.

It is known that the coding of reward is crucially involved in action selection and is therefore also intrinsic to goal-directed behaviour (Schultz, 2000). Activity in the mirror neuron system and the action observation network has been shown to be specific only to observed actions that are goal-directed (Rizzolatti et al., 1996). Therefore it follows that reward and punishment are likely to have reciprocal interaction effects with the neural activity associated with action observation, and consequently may also influence the degree to which action understanding and observational learning take place, as Bandura already pointed out in his pioneering behavioural experiments. However, it is not clear as to how reward or punishment is associated with actions and the outcomes of others' actions, and how this may eventually affect motor activity induced while observing others in a social setting. To the best of our knowledge, there has not yet been systematic experimental work carried out that has investigated if and how reward or punishment could modulate neural activity in the action observation network.

The propensity for social context to cause differences in motor activity in the mirror system, and the corresponding mu suppression, is still debated. It is also still unclear as to what specific functional relevance this neural activity has on social cognitive processes, and how reward or punishment may interact with processing others' actions. The primary aim of this study was to compare the mu rhythm suppression during observation of actions that are rewarding, punishing or neutral for the observer. As a secondary aim, we also wanted to explore the effect of perspective on the mu suppression. Finally we were also interested in better characterizing the temporal dynamic associated with changes in the mu rhythm, in relation to the different processing stages during action observation, given that previous EEG studies have typically overlooked the temporal component of the mu suppression. It was hypothesised that when rewards are associated with observed actions, this would induce greater mu rhythm suppression as opposed to punishing and neutral actions. It was also predicted that actions seen from a 1st-person perspective would lead to greater mu suppression, as compared to actions observed from a 3rd-person perspective.

2. Methods

2.1. Participants

17 right-hand dominant (according to the Edinburgh Handedness Inventory (Oldfield, 1971)) females were recruited from the Psychology Departments of Ghent University, Belgium. The mean age of participants was 20.3 years (SD = 1.99) and individuals with a history of neurological damage or psychiatric illness were excluded. Informed consent was acquired from all subjects before the experimental procedure began.

2.2. Design

Participants sat with their hands positioned on a table and head movements were restrained by a chin rest placed in front of a computer screen. The stimuli consisted of a set of videos, with each video showing a single action performed by a person seen from either an egocentric (1^{st}-person) or allocentric (3^{rd}-person) perspective. All videos depicted 5 bowls on a table; three colored bowls arranged across the middle of the table, and two colorless bowls, one in front of each performer. The three colored bowls were arranged on the table along one plane and were all approximately equidistant from the performers, and from each other. In each video, a single coin was transferred from the performer's bowl to one of the three colored bowls in the middle of the table. Each of the three colored bowls were labeled (using an inset superimposed on the video) with a "+", "-" and "0" sign, referring to rewarding, punishing and neutral actions, respectively. This therefore resulted in a 2 (1^{st} and 3^{rd} person perspective) x 3 (reward, punishment or neutral) factorial design. To control for unwanted spatial effects, 6 different spatial configurations of the superimposed "+", "-" and "0" signs were created using the same original videos. This manipulation was introduced to cancel out systematic differences in the kinematics across the three conditions, i.e. transferring coins to the center or left or right-side bowls, with an equal probability across the three conditions. Participants were randomly assigned to one of these 6 video sets, such that spatial configuration effects were neutralized across participants. All videos were filmed from the same perspective, and actions were performed either by the person sitting behind the camera (1^{st}-person), or by the person facing the camera (3^{rd}-person). When actions were performed in the egocentric perspective, only the hands and arms of the performer were visible.

In total, 120 videos were presented in each testing session in a pseudorandom order in 6 blocks, with a single video constituting a single trial, and a single action. This made 20 trials per condition in each testing session. The main trials were preceded by a block of 8 practice trials. A fixation cross was presented for one second before each video. Each video lasted for 11 sec, with movement onset at 1 sec after the start of the video. The performer in the video started the movement from the same resting position that the participant was instructed to be in, and returned to this position at movement offset. The movement lasted for 6 sec and following movement offset, the video continued for a further 4 sec, with the performer staying in the resting position.

2.3. Procedure

Participants watched the video clips, which depicted two people sitting at a table and transferring coins from one bowl to one of three other bowls. Participants were told that each time an object was transferred to the "+" bowl, they would win one euro (rewarding), when an object was put into the "-" bowl, they would lose one euro (punishing), and when transferred to the "0" bowl there was no change (neutral). Participants were asked to only sit still, watch and count the number of coins transferred to each bowl and consequently the amount of money they would win or lose.

Participants were told that they started with €20 "in the bank", which would fluctuate according to the number of rewarding and punishing actions observed, so they would have to keep count of their money "in the bank", and would be given the final counted amount at the end of the experiment. After each block of trials, participants were asked to report the amount of money "in the bank". This was done to ascertain a balanced level of attention across the three conditions and allowed for the possibility of excluding data for any trials in which the participant did not pay close enough attention to report the correct amount. However, as it turned out, all participants always reported the correct amount of money, suggesting that they correctly paid attention to the individual videos, regardless of the actual reward-related condition. Participants were also asked to rate the previously seen action for subjective pleasantness, arousal and how easy it was to pay attention according to a visual analogue scale from 0 to 10 (except for the pleasantness rating, which was rated from-10 to 10, with -10 being “very unpleasant” and 10 being “very pleasant”). This was done after each of the 6 blocks of trials, and consequently, all action conditions were rated by the end of the testing session. Only the lowest and highest scores were indicated on the scale, with a dotted line between the two on which participants were asked to mark their response with a cross.

According to visual inspection of the video stimuli, a critical 3 sec epoch during the observed action was selected for the mu rhythm analysis, in which the reward-related conditions (reward, punishment or neutral) differ i.e. when the action begins to diverge to one of the rewarding, punishing or neutral bowls. The video stimuli did not differ across conditions before this 3 sec time window, nor after.

2.4. EEG data acquisition

EEG was recorded from 64 channels with a BioSemi ActiveTwo system at a sampling rate of 2,048 Hz but was later down sampled offline to 512 Hz. The 64 electrode positions were distributed over the scalp according to the international 10-20 EEG system. An additional electrode was placed above the right eye in line with the pupil (vertical EOG), plus one placed at the outer canthus (horizontal EOG). According to the BioSemi criteria, the predetermined electrode locations CMS and DRL served as the reference and ground electrodes, respectively. Following acquisition, the raw data were processed offline with BrainVision Analyzer 2 (Brain Products GmbH). Firstly, the data was visually inspected and channels that were particularly noisy were identified, removed and later topographically interpolated. The data was then re-referenced to all electrodes and submitted to a band-pass filter of 0.1 Hz to 30 Hz, with a 50 Hz notch filter applied. Ocular correction was performed with the vertical EOG.

2.5. Data analysis

2.5.1 Behavioural data

Each score on the visual analogue scale for the subjective rating of arousal and attention was calculated by measuring the distance from the start of the dotted line to the point at which participants had marked a cross. For the subjective rating of pleasantness, a mid-point on the scale was measured and taken as the zero point, with responses falling to the left of the zero point representing negative scores, and those to the right being positive. For each question, the mean score was taken for all rewarding, punishing and neutral actions. Paired t-tests were later performed between scores on all conditions for each question. A correlation analysis was also performed to investigate whether scores of pleasantness, arousal and attention related independently to the mu suppression.

2.5.2. Mu rhythm

The mu suppression was extracted from the central electrodes overlaying sensorimotor cortex; electrode positions C3, C1, Cz, C2, and C4. Baseline and action observation epochs were first determined. For the baseline for mu extraction, the 1 sec epoch preceding movement onset (after video onset) was used as the baseline for mu extraction (as Schuch et al., 2010). The 3 sec action observation critical epoch was segmented into 1 sec segments, and further analysis was done with these 1 sec segments. EEG artifacts were identified and rejected if they exceeded ±100 µV. A Fast Fourier Transform (FFT) with a 10 % Hamming window was performed separately on each of the 1 sec baseline and action observation epochs and an average was then taken for each condition, and consequently powers in the alpha frequency band (8-13Hz) were exported. To calculate the mu suppression, and control for individual variability in alpha power, a natural log transform (ln) was calculated for the ratio of the power of the alpha band of the action observation condition over the baseline condition epochs accordingly (Oberman et al., 2005; Raymaekers et al., 2009).

Repeated measures ANOVA was used with the exported log ratio mu rhythm suppression values with the reward-related conditions (rewarding, punishing, neutral) and electrode position (C1, C2, C3, C4, Cz) as within-subject factors. Pair-wise comparisons were conducted for significant main effects (fig.

1b). The appropriate assumptions for performing an ANOVA had been checked for. Whole-head topographical plots were acquired with the mapping function of BrainVision Analyzer 2 by selecting the 8-13Hz frequency band for all electrodes following an FFT of the same 3 sec segment used for the mu rhythm extraction. These were then averaged across subjects for the reward-related conditions.

2.5.3. Time-course analysis of mu power

To calculate the dynamic change in mu power (8-13 Hz) during the course of the video, averages were taken for each consecutive 500 msec segment from the start to the end of the video. This was done for each reward-related condition (see Fig. 2). A post-hoc analysis was done on the 3 sec epoch used for the mu rhythm analysis, which was split into three 1 sec epochs. Paired t-tests were performed to compare differences between each condition in each of the three 1 sec epochs.

3. Results

3.1. Behavioral data

Results show that the subjective ratings of pleasantness are congruent to the reward-related conditions (Fig. 1a), with rewarding actions being judged as the most pleasant, and punishing the least. Paired comparisons reveal significant differences between pleasantness ratings of rewarding and punishing ($t(16)=4.59$, $p<0.001$), rewarding and neutral ($t(16)=5.18$, $p<0.001$), and punishing and neutral actions ($t(16)=-2.38$, $p=0.03$). It is also evident from subjective ratings of arousal that rewarding actions are more arousing than neutral actions ($t(16)=3.23$, $p=0.005$). Importantly, the ratings demonstrate that differences between reward-related conditions were not accounted for by differences in attention, showing no significant differences between conditions. It is also worth noting that the correlation analyses revealed no significant correlations between behavioral ratings of pleasantness, arousal nor attention with the mu suppression.

3.2. Mu rhythm

As recent research has shown that beta band activity over sensorimotor cortex may also be dynamically modulated during action observation (Press et al., 2011), analyses were repeated for the beta band (15-25Hz) to compare the power across conditions. However, no significant experimental effects were found in the beta band and therefore, the rest of the article refers only to EEG data in the alpha frequency band. Non-significant effects were found for perspective conditions (F (1,16)=1.50, p=0.24), and for the interaction between reward-related conditions and perspective (F (2,15)=0.21, p=0.82). Therefore, perspective conditions were not included in any of the further analyses as egocentric and allocentric perspective conditions were pooled together.

Significant main effects for the EEG mu rhythm suppression were found among the three reward-related conditions (F(2,15)=3.74, p=0.05) and six electrodes (F(4,13)=4.22, p=0.02). Pairwise comparisons between reward-related conditions showed significant differences between rewarding and punishing actions (t(16)=-2.15, p=0.05) and rewarding and neutral actions (t(16)=-2.36, p=0.03), however there was no significant difference between punishing and neutral actions (t(16)=-1.42, p=0.17). Figure 1b shows the mu rhythm suppression for each reward-related condition (rewarding, punishing, and neutral) pooled over the electrodes covering sensorimotor cortex, and over perspective conditions (egocentric and allocentric). The largest mu suppression was found for rewarding and the smallest for neutral actions (Fig. 1b). Topographical maps of the mu power (Fig. 1b) including all 64 channels demonstrated substantial suppression predominantly over medial frontal and sensorimotor areas, and most importantly, with little overlap between the two.

--- Insert Figure 1a) and 1b) about here ---

3.3. Time course analysis of mu power

Remarkably, a closer look at the time course of the mu power effect (Fig. 2) revealed a significant suppression at video onset, followed by a second significant suppression around 3.5 to 4 sec after video onset. In addition to this, the time-plot revealed an asymmetry between reward conditions following this second suppression. Post-hoc comparisons confirmed this asymmetry whereby, in the first second of the critical 3 sec epoch, rewarding actions were significantly different from neutral ($t(16)=2.65$, $p=0.02$) and punishing actions ($t(16)=2.61$, $p=0.02$),whereas no significant difference was found between punishing and neutral actions ($t(16)=0.66$, $p=0.52$).The difference between punishing and neutral actions only reached significance during the third second of this critical epoch ($t(16)=2.12$, $p=0.05$), and therefore demonstrating a later and more prolonged mu suppression for punishing than rewarding actions.

--- Insert Figure 2 about here ---

4. Discussion

In the present study, we sought to examine the effect of reward and punishment on brain activity in an action-observation paradigm. We predicted that mu-rhythm suppression would be greater in the rewarding, relative to the punishing and neutral conditions, and that the observed effect would be larger in the 1st, as opposed to 3rd -person condition. In partial support of our predictions, the main finding of our study reveals reward-related modulation of motor cortex activity, as indexed by systematic changes in the mu rhythm suppression, when seeing others' actions. When one observes others' actions, it appears that there is greater motor resonance if the consequence of the action is associated with a reward for the observer, whereas actions associated with punishment induced less motor resonance. Importantly, observed actions that did not lead to a reward or punishment, i.e. were embedded in a neutral context, induced comparatively the least motor cortex activity. When looking at the distribution of the mu suppression over the whole scalp (topographic mapping), it appears that the reward-related effects were primarily driven by suppression over sensorimotor areas, as opposed to more posterior occipital areas. Hence this analysis rules out the possibility that the effects reported in this study were somehow confounded by systematic changes in attention-based posterior alpha. Our behavioural results also provide further evidence that the effect of the reward manipulation was not driven by attentional differences. Considering the lack of modulation by reward-related conditions found in the beta frequency band, our data seems to show that this effect is specific to mu rhythm in the alpha band. We also hypothesised that a difference in perspective-taking (egocentric vs. allocentric) would have an influence on the expression of the mu suppression; however our results did not confirm this prediction, in contrast to some previous studies (Libby et al., 2009). Interestingly, our analysis of the temporal dynamic of the mu rhythm revealed a second suppression component arising as a result of the reward-related condition effect. This extends earlier mu suppression studies that have primarily looked at the (pooled) average mu suppression over the whole period of the observed action, and therefore reported only an overall single suppression component during action observation, which may have potentially blurred some important differences in the time-course of the mu suppression. Finally, we show that mu suppression occurred later for punishing actions than rewarding ones. Even though punishing actions induced greater mirror motor activity than neutral actions, it appears that punishing actions are associated with a somewhat delayed and prolonged mirror motor response, which would have been missed if the temporal dynamic changes in the mu power had not been taken into consideration.

The outcome of our study has implications for a broad range of themes in social cognition and also raises a number of important methodological and theoretical considerations for future research in this area. As already pointed out here above, the influence of reward and punishment on observational learning has been primarily investigated at the behavioural level; hence our study is the first providing direct neuroscientific evidence for this link. According to our results, action understanding, imitation and observational learning may be driven by the associations made between rewards, punishments and the observed actions, due to differences in motor resonance in the motor cortex.

In light of these results, we suggest that some previous findings demonstrating contextual differences in mu rhythm suppression and mirror neuron-related activity could in fact have arisen because of uncontrolled differences in the reward value associated with the observed actions across the different contexts and/or experimental conditions. In the social domain, findings from studies comparing social and non-social stimuli (Pineda & Hecht, 2009), with the aim of deconstructing the social relevance of the mirror motor system, could be accounted for by the intrinsic reward that may be associated with social stimuli and social interaction, as opposed to stimuli devoid of any social meaning or value that may be inherently less rewarding. In other words, the social interaction in itself may be rewarding to the observer, as suggested by some authors (Krach et al., 2010). This may also be relevant to studies which have found that the social relationship between the observer and the performer may influence mirror neuron activity (Liew et al., 2010). The reward value attributed to the observed action can depend upon the relationship between confederates in a social interaction, such as that demonstrated by in-group vs. out-group differences (Gutsell & Inzlicht, in press), and competitive vs. cooperative scenarios (Koban et al., 2010). Different social contexts will induce different degrees of reward associated with others' actions, which could depend upon a wide variety of personal and interpersonal motivational factors. The magnitude of mu suppression during the observation of actions is also enhanced when the observed action inflicts pain on the performer (Perry et al., 2010a), which incidentally could be comparable to the effect of punishment in our study, when compared to neutral actions. The magnitude of reward and punishment that the observer associates with the observed action, or the consequences of the observed action, could modulate the degree to which one eventually empathises with others and shares others' intentions or concerns.

It has been proposed that selective dysfunctions of the mirror system may play a key role in the genesis and maintenance of pathological deficits in social cognition (Buccino et al., 2008), particularly in autism spectrum disorders (ASDs) (Williams et al., 2001), Williams Syndrome (Tager-Flusberg,

2000) and schizophrenia (Singh et al., 2011; McCormick et al., 2012). Arbib & Mundhenk (2005) extended this proposal and suggested that dysfunctions in the mirror neuron system may also contribute to deficits in self-monitoring in schizophrenia. Pathological conditions that express deficits in social cognition and social functioning have also been found to have underlying abnormalities in reward-processing, including ASDs (Dichter et al., 2012; Scott-Van Zeeland et al., 2010) and schizophrenia (Gold et al., 2008). It may be the case that in such clinical populations, patients may have abnormal experiences of reward and punishment from social stimuli, caused by an underlying general breakdown in reward-processing. Alternatively it may be the converse in that cognitive deficits in processing social stimuli, or a lack of preference for social stimuli, may have a deleterious effect on the ability to experience social stimuli as being “intrinsically” rewarding. Either way, our results could help better explain some earlier discrepant findings in the literature comparing mu rhythm suppression in clinical and non-clinical populations (Raymaekers et al., 2009). In light of this, deficits in reward processing may therefore play a causal role in the development and maintenance of pathological deficits in social cognition.

Motor acts are dynamic processes during which the contextual online changes in the observer’s motor cortex activity are likely to reflect the associated contextual changes during the dynamics of the observed action. Schuch and colleagues (2010) were among the first to look at the dynamic changes in mu suppression over the time course of the whole observed action. From their results, it appears that there is only one substantial suppression of the mu rhythm, occurring at the time in which the action-related object is presented on screen. This initial suppression may be an index of an anticipatory motor response to the forthcoming action, as possibly also reflected in our results, because expectation or anticipation of the forthcoming action was high due to the regular timing of stimulus onset on each trial. The second suppression seen in the dynamic change in the mu rhythm power in our results provides evidence for an additional and independent mu suppression component, evoked by the outcome of the action, which may be specifically associated to the context of the action.

The apparent delayed mu suppression seen for punishing actions is a new and puzzling finding. This effect could be a demonstration of some kind of aversion to the negative consequences of others' actions, in which there may be an active inhibition of motor cortex somehow causing a slower return to baseline activity. This finding is in line with the early work of Bandura whereby the association of punishment with the observed action led to discouragement of imitative behaviour. Therefore, this result provides evidence for the dynamic interplay between action observation and motivational drives, suggesting an online modulation of action understanding depending on the specific reward-related factors involved and perceived in the social setting at a given moment in time. Hence, our findings show that mirror motor activity during action observation does not correspond only to a single or unique motor resonance process, but differential effects in the neurophysiological time-course and expression may be revealed depending on situational changes in affective or motivational factors, suggesting a more fine-grained temporal dynamic for the mu suppression than previously thought. These findings also highlights the importance of looking at the online dynamic changes in brain activity over time, as a more ecologically valid approach to study social interaction, to gain more insight into how our brains respond to the dynamic changes in our environment.

5. Conclusion

It is still debated as to what degree the mirroring motor system is engaged in action understanding. The modulation of reward and punishment on the motor mirroring system adds further support to the notion that the mirror system does actually contribute to the understanding of others' goals and intentions. Furthermore, this also provides neuroscientific support to Bandura's original behavioural experiments that already highlighted the central role of reward and punishment during observational learning. Future studies therefore may need to consider the potential confounding effects of the associated reward on the observed action in the experimental condition of interest, and the reward-related associations of actions created by different contexts, whether it is social or not. Moreover, further studies exploring the mu rhythm suppression in action observation should also seek to dissociate the dynamic changes in neural activity when making inferences about social interaction, which reflect the dynamic changes in the environment that occur in everyday social interaction. In light of our new results, these differential “simulated” motor effects may stem from fundamental situational differences in the processing of reward or punishment, or the perceived reward-value attributed to others’ actions, rather than ‘social’ processing per se or motor simulation alone. Psychosocial interventions that rely on imitative and observational learning may need to consider whether an underlying deficit in the processing of reward could interfere with the ability to learn by observation. In these cases, deficits in reward processing could also have a detrimental effect on the capacity for motor simulation, and therefore also limit the capacity for social learning and the development of social skills in childhood and also potentially persisting into adulthood. The reward or punishment associated with others’ actions is likely to influence the capacity for understanding others’ actions, their goals and intentions, and therefore will also directly influence the potential for social observational learning, or its selective breakdown, in specific pathological conditions such as ASDs and schizophrenia.

References:

Arnstein, D., Cui, F., Keysers, C., Maurits, N.M., Gazzola, V. (2011). Mu-suppression during action observation and execution correlates with BOLD in dorsal premotor, inferior parietal, and SI cortices. *The Journal of neuroscience : the official journal of the Society for Neuroscience,* 31 (40): 14243-14249.

Bandura, A. (1977). *Social learning theory*. Prentice Hall: Englewood Cliffs, N.J.

Blakemore, S.J., Frith, C. (2005). The role of motor contagion in the prediction of action. *Neuropsychologia,* 43 (2): 260-267.

Buccino, G., Amore, M. (2008). Mirror neurons and the understanding of behavioural symptoms in psychiatric disorders. *Current opinion in psychiatry* 21 (3): 281-285.

Dichter, G.S., Richey, J.A., Rittenberg, A.M., Sabatino, A., Bodfish, J.W. (2012). Reward circuitry function in autism during face anticipation and outcomes. *Journal of autism and developmental disorders,* 42 (2): 147-160, 2012.

Gallese, V., Fadiga, L., Fogassi, L., Rizzolatti, G. (1996). Action recognition in the premotor cortex. *Brain : a journal of neurology,* 119 (Pt 2): 593-609.

Gallese, V. (2003). The manifold nature of interpersonal relations: the quest for a common mechanism. *Philosophical transactions of the Royal Society of London. Series B, Biological sciences,* 358 (1431): 517-528.

Gallese, V., Keysers, C., Rizzolatti, G. (2004). A unifying view of the basis of social cognition. *Trends in cognitive sciences,* 8 (9): 396-403.

Gold, J.M., Waltz, J.A., Prentice, K.J., Morris, S.E., Heerey, E.A. (2008). Reward processing in schizophrenia: a deficit in the representation of value. *Schizophrenia bulletin* 34 (5): 835-847.

Gutsell, J.N., & Inzlicht, M. (in press). Using EEG mu-suppression to explore group biases in motor resonance. In B. Derks, D. Scheepers and N. Ellemers (Eds.). *The Neuroscience of Prejudice*. London: Psychology Press.

Hari, R. (2006). Action-perception connection and the cortical mu rhythm. *Progress in brain research,* 159: 253-260.

Jeannerod, M., Anquetil, T. (2008). Putting oneself in the perspective of the other: a framework for self-other differentiation. *Social neuroscience,* 3 (3-4): 356-367.

Keysers, C., Gazzola, V. (2006). Towards a unifying neural theory of social cognition. *Progress in brain research,* 156: 379-401.

Kilner, J.M., Marchant, J.L., Frith, C.D. (2006). Modulation of the mirror system by social relevance. *Social cognitive and affective neuroscience,* 1 (2): 143-148.

Koban, L., Pourtois, G., Vocat, R., Vuilleumier, P. (2010). When your errors make me lose or win: event-related potentials to observed errors of cooperators and competitors. *Social neuroscience,* 5 (4): 360-374.

Krach, S., Paulus, F.M., Bodden, M., Kircher, T. (2010). The rewarding nature of social interactions. *Frontiers in behavioral neuroscience,* 4: 22.

Libby, L.K., Shaeffer, E.M., Eibach, R.P. (2009). Seeing meaning in action: a bidirectional link between visual perspective and action identification level. *Journal of experimental psychology. General*, 138 (4): 503-516.

Liew, S.L., Han, S., Aziz-Zadeh, L. (2010). Familiarity modulates mirror neuron and mentalizing regions during intention understanding. *Human brain mapping,* 32 (11): 1986-1997.

McCormick, L.M., Brumm, M.C., Beadle, J.N., Paradiso, S., Yamada, T., Andreasen, N. (2012). Mirror neuron function, psychosis, and empathy in schizophrenia. *Psychiatry research,* 201 (3): 233-239.

Mitchell, J.P. (2009). Inferences about mental states. *Philosophical transactions of the Royal Society of London. Series B, Biological sciences,* 364 (1521): 1309-1316.

Mukamel, R., Ekstrom, A.D., Kaplan, J., Iacoboni, M., Fried, I. (2010). Single-neuron responses in humans during execution and observation of actions. *Current biology,* 20 (8): 750-756.

Oberman, L.M., Hubbard, E.M., McCleery, J.P., Altschuler, E.L., Ramachandran, V.S., Pineda, J.A. (2005). EEG evidence for mirror neuron dysfunction in autism spectrum disorders. *Brain research. Cognitive brain research,* 24 (2): 190-198.

Oberman, L.M., McCleery, J.P., Hubbard, E.M., Bernier, R., Wiersema, J.R., Raymaekers, R., Pineda, J.A. (2012). Developmental changes in mu suppression to observed and executed actions in autism spectrum disorders. *Social cognitive and affective neuroscience*. doi: 10.1093/scan/nsr097.

Oldfield, R.C. (1971). The assessment and analysis of handedness: The Edinburgh inventory. *Neuropsychologia*, 9: 97-113.

Perry, A., Bentin, S., Bartal, I.B., Lamm, C., Decety, J. (2010a). "Feeling" the pain of those who are different from us: Modulation of EEG in the mu/alpha range. *Cognitive, affective & behavioral neuroscience,* 10 (4): 493-504.

Perry, A., Troje, N.F., Bentin, S. (2010b). Exploring motor system contributions to the perception of social information: Evidence from EEG activity in the mu/alpha frequency range. *Social neuroscience,* 5 (3): 272-284.

Perry, A., Stein, L., Bentin, S. (2011). Motor and attentional mechanisms involved in social interaction--evidence from mu and alpha EEG suppression. *NeuroImage,* 58 (3): 895-904.

Pineda, J.A., Hecht, E. (2009). Mirroring and mu rhythm involvement in social cognition: are there dissociable subcomponents of theory of mind? *Biological psychology,* 80 (3): 306-314.

Press, C., Cook, J., Blakemore, S.J., Kilner, J. (2011). Dynamic modulation of human motor activity when observing actions. *Journal of Neuroscience,* 31 (8): 2792-2800.

Raymaekers, R., Wiersema, J.R., Roeyers, H. (2009). EEG study of the mirror neuron system in children with high functioning autism. *Brain research,* 1304: 113-121.

Rizzolatti, G., Fadiga, L., Gallese, V., Fogassi, L. (1996). Premotor cortex and the recognition of motor actions. *Brain research. Cognitive brain research,* 3 (2): 131-141.

Rizzolatti, G., Fogassi, L., Gallese, V. (2001). Neurophysiological mechanisms underlying the understanding and imitation of action. *Nature reviews Neuroscience,* 2 (9): 661-670.

Schuch, S., Bayliss, A.P., Klein, C., Tipper, S.P. (2010). Attention modulates motor system activation during action observation: evidence for inhibitory rebound. *Experimental brain research,* 205 (2): 235-249.

Schultz, W. (2000). Multiple reward signals in the brain. *Nature reviews Neuroscience,* 1 (3): 199-207.

Scott-Van Zeeland, A.A., Dapretto, M., Ghahremani, D.G., Poldrack, R.A., Bookheimer, S.Y. (2010). Reward processing in autism. *Autism research : official journal of the International Society for Autism Research,* 3 (2): 53-67.

Tager-Flusberg, H., Sullivan, K. (2000). A componential view of theory of mind: evidence from Williams syndrome. *Cognition,* 76 (1): 59-90.

Williams, J.H., Whiten, A., Suddendorf, T., Perrett, D.I. (2001). Imitation, mirror neurons and autism. *Neuroscience and biobehavioral reviews,* 25 (4): 287-295.

Woodruff, C.C., Martin, T., Bilyk, N. (2011a). Differences in self- and other-induced Mu suppression are correlated with empathic abilities. *Brain research,* 1405: 69-76.

Woodruff, C.C., Daut, R., Brower, M., Bragg, A. (2011b). Electroencephalographic alpha-band and beta-band correlates of perspective-taking and personal distress. *Neuroreport* 22 (15): 744-748.

Acknowledgements:

This study was supported by an International Brain Research Organisation (IBRO)-CEERC-WERC InEurope Travel Fellowship granted to the author ECB. The author GP is supported by grants from the European Research Council (Starting Grant #200758) and Ghent University (BOF Grant #05Z01708).

Competing interests statement:

The authors declare no competing financial interests.

Figure captions (color required):

Figure 1:

a) **a) Subjective ratings for pleasantness, arousal and attention for rewarding, punishing and neutral observed actions:** Ratings made along a continuous visual analogue scale, with pleasantness rated from -10 to 10 and arousal and attention from 0 to 10. (*=p<0.05; **=p<0.01; n.s.=p>0.05)

b) **b) EEG mu rhythm suppression (log ratio relative to the baseline) for rewarding, punishing and neutral conditions:** pooled over electrodes C3, C1, Cz, C2 and C4 (*=p<0.05) during the observation of the action. Topographical maps of the distribution of mu power over the whole head (darker areas represent a lower mu power) are also presented above the bar chart.(*p<0.05; n.s.=p>0.05)

Figure 2:

Time course analysis of the EEG mu rhythm: Plot showing the change in EEG mu power (8-13Hz), averaged from electrodes over sensorimotor areas (C3, C1, Cz, C2 and C4) over the course of the video stimulus, showing the different reward conditions. The critical 3s time window selected for the mu rhythm suppression analysis (Fig. 1b)) is also highlighted here between 4s and 7s.Stills taken from the video stimuli are presented along the time axis. The dotted vertical lines mark the 1 s epochs used to compare the latency of the mu suppression between conditions.

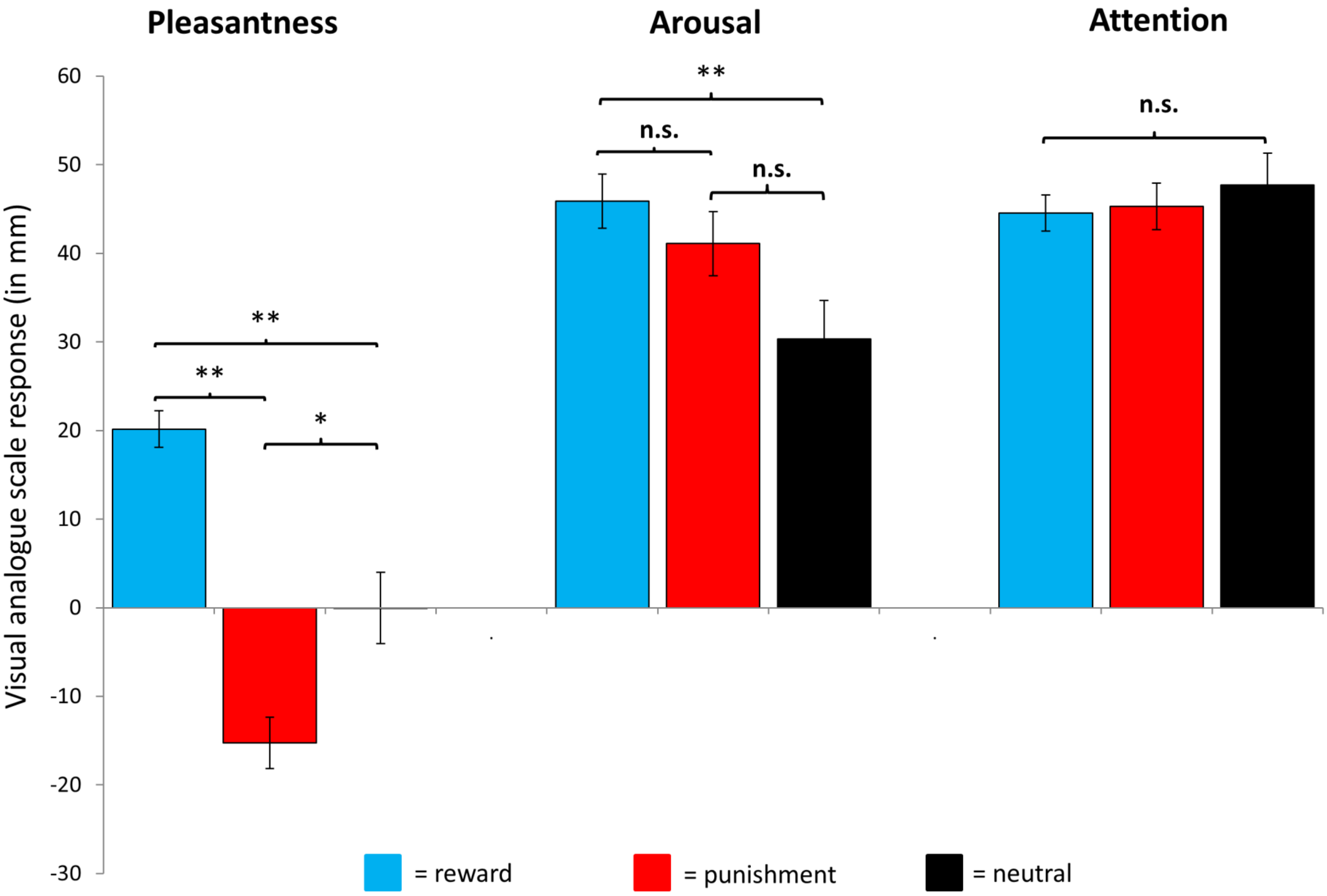
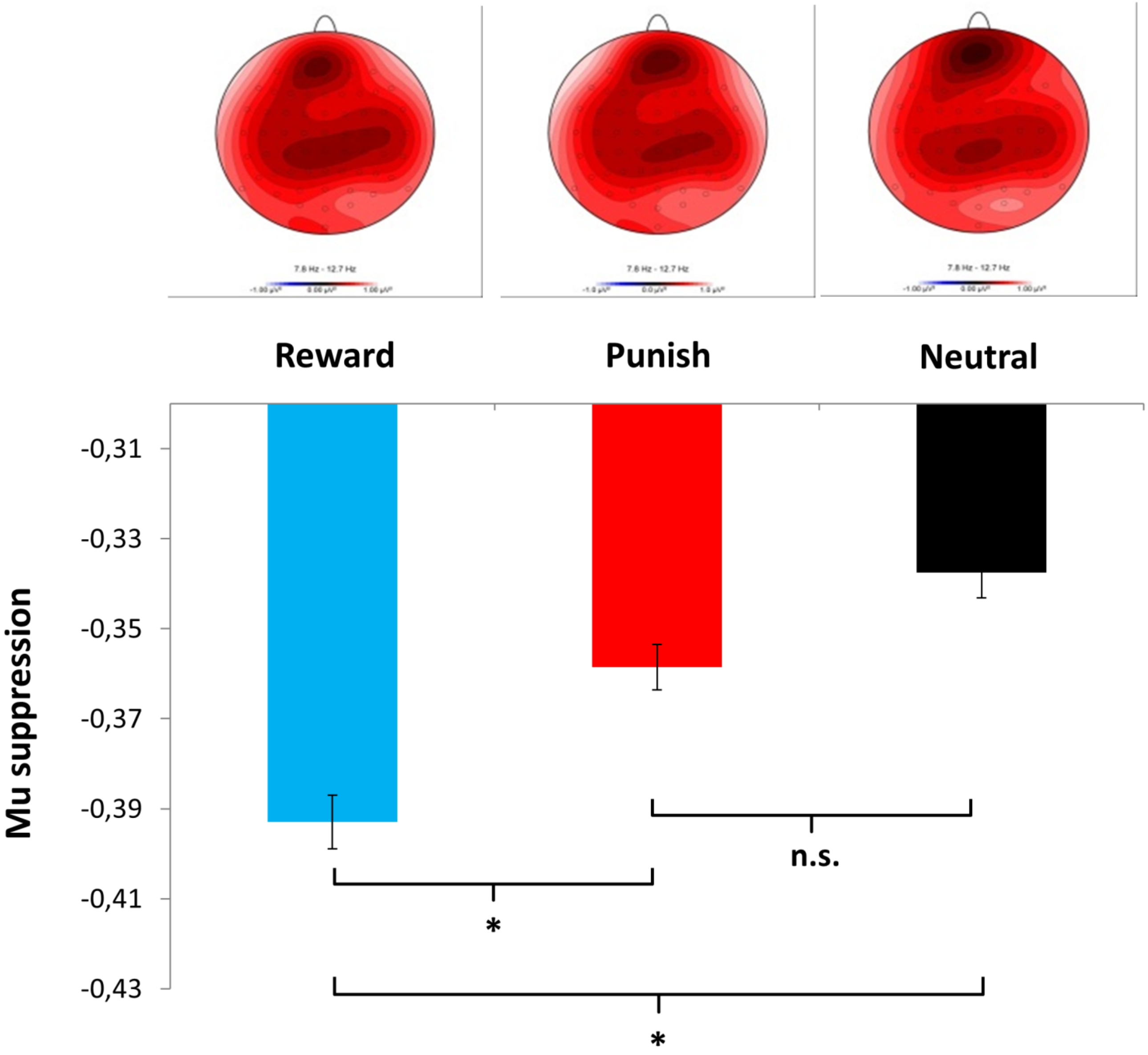

Pleasantness
Arousal
Attention
Visual analogue scale response (in mm)
60
50
40
30
20
10
0
-10
-20
-30
**
**
*
**
n.s.
n.s.
n.s.
= reward
= punishment
= neutral

Figure 1a



7.8 Hz - 12.7 Hz
-1.00 µV²
0.00 µV²
1.00 µV²
7.8 Hz - 12.7 Hz
-1.0 µV²
0.0 µV²
1.0 µV²
7.8 Hz - 12.7 Hz
-1.00 µV²
0.00 µV²
1.00 µV²
Reward
Punish
Neutral
Mu suppression
-0,31
-0,33
-0,35
-0,37
-0,39
-0,41
-0,43
n.s.
*
*

Figure 1b

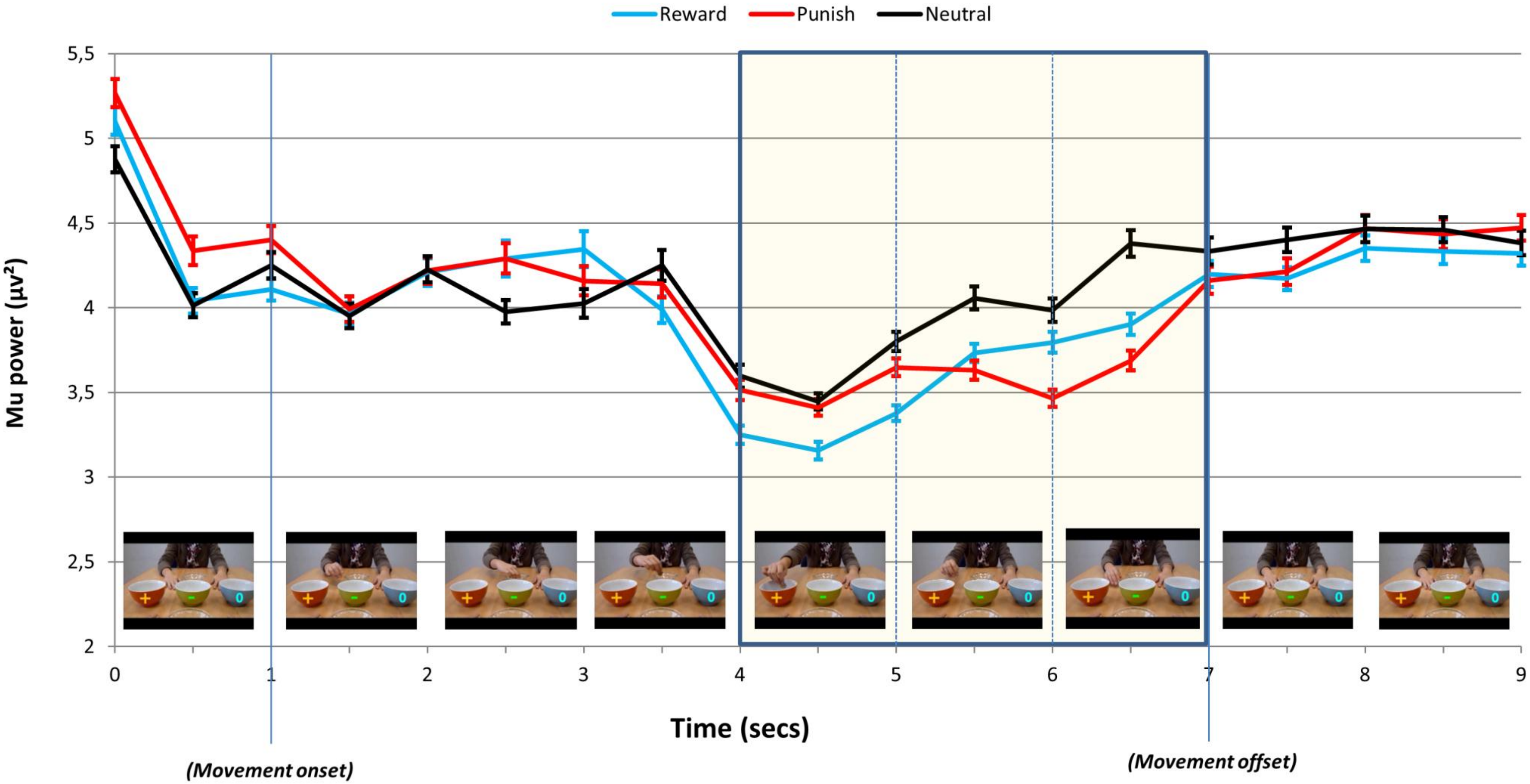

Reward
Punish
Neutral
Mu power (μv²)
5,5
5
4,5
4
3,5
3
2,5
2
0
1
2
3
4
5
6
7
8
9
Time (secs)
(Movement onset)
(Movement offset)
+
-
0

Figure 2