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SOCIAL REWARD IN ACTION: REWARD MAGNITUDE AND VALENCE EFFECTS ON THE EEG MU RHYTHM

EYLEM İÇERİSİNDE SOSYAL ÖDÜLLER: ÖDÜL BÜYÜKLÜĞÜ VE DEĞER ETKİSİNİN MÜ AKTİVİTESİ ÜZERİNE ETKİSİ

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Abstract

In social interactions, the values we associate with observed actions can influence how we process others' behaviors and the decisions we make. Some studies have suggested that different social contexts, and particularly the reward value of perceived actions can modulate motor system activity when observing others' actions. However, sensitivity to reward magnitude has never been tested in the action observation system. Here we used electroencephalography (EEG) to investigate the independent effects of reward valence and magnitude on the mu rhythm, an index of the motor mirror system, while participants (N=23) passively observed actions that led to high or low rewards or losses. Behavioral measures of social approach/avoidance, theory of mind and empathy were also taken. Results showed that reward valence significantly modulated mu rhythm, where losses led to greater mu suppression, but reward magnitude had no effect. The findings also demonstrated a novel association between the specific reward-related modulation of the mu rhythm and social cognitive skills, particularly cognitive empathy and emotional reactivity. This study provides further evidence for the role of reward processing in the mirror motor system, and highlights the relationship between value-based action perception and social cognitive traits, implicating a role for the mirror system in social decision-making.

Keywords: mu rhythm; action observation; EEG; mirror neurons; reward; social context

Özet

Sosyal etkileşimlerde, gözlemlenen eylemlerle ilişkilendirdiğimiz değerler, başkalarının davranışlarını ve aldığımız kararları nasıl yorumladığımızı etkileyebilir. Bazı araştırmalar, farklı sosyal bağlamların ve özellikle de algılanan eylemlerin ödül değerinin, başkalarının eylemlerini gözlemlerken motor sistem aktivitesini düzenleyebileceğini öne sürmektedir. Bununla birlikte, ödül büyüklüğüne olan duyarlılık, eylem gözlem sistemi boyutunda hiçbir zaman test edilmemiştir. Burada, katılımcıların (N = 23) pasif olarak yüksek veya düşük ödüllere veya kayıplara yol açan eylemleri gözlemlerken, ödül ritim değerinin ve büyüklüğünün mu ritm üzerindeki bağımsız etkilerini ve motor ayna sisteminin bir endeksini araştırmak adına elektroensefalografi (EEG) kullandık. Sosyal yaklaşım / kaçınma, zihin teorisi ve empatinin davranışsal ölçümlemeleri de alınmıştır. Sonuçlar, ödül değerliliğinin, kayıpların daha büyük mu süpresyona yol açtığını, ancak ritmin büyüklüğünün etkili olmadığını ve mu ritmde önemli ölçüde modüle olduğunu gösterdi. Elde edilen bulgular, mu ritim ve sosyal bilişsel beceriler arasında, özellikle bilişsel empati ve duygusal reaktivite ile ilgili ödül ile ilgili modülasyon arasında yeni bir ilişki olduğunu göstermiştir. Bu çalışma, ayna motor sistemindeki ödül işleme rolüne ilişkin daha fazla kanıt sunmakta ve değer bazlı eylem algısı ile sosyal bilişsel özellikler arasındaki ilişkiyi vurgulamakla birlikte toplumsal karar almada ayna sisteminin rolünü vurgulamaktadır.

Anahtar Kelimeler: *mu ritmi; aksiyon gözlemi; EEG, ayna nöronlar; ödül; sosyal içerik*

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1. Introduction

A crucial component required for successful social interaction involves the encoding of others' actions and intentions. The ability to learn from others' actions is critical for the development of social cognitive skills through interactive experiences early in life (Cook, Bird, Catmur, Press, & Heyes, 2014). The discovery of the mirror neuron system in primates, in which specific neurons fire during both the execution and observation of an action (Gallese, Fadiga, Fogassi, & Rizzolatti, 1996; Rizzolatti, Fadiga, Gallese, & Fogassi, 1996), led to suggestions that others' actions are mapped onto one's own sensorimotor cortices (Keysers & Gazzola, 2006). There is much evidence to suggest that a comparable neural system exists in humans, which has common functional characteristics as the monkey mirror system (Bimbi et al., 2018; Chong, Cunnington, Williams, Kanwisher, & Mattingley, 2008; Kilner, Neal, Weiskopf, Friston, & Frith, 2009; Molenberghs, Cunnington, & Mattingley, 2012; Mukamel, Ekstrom, Kaplan, Iacoboni, & Fried, 2010; Press, Weiskopf, & Kilner, 2012). Subsequent studies have identified modulations of the mu-rhythm to be a possible electrophysiological marker of the putative human mirror system (hMS), which could provide insight into the underlying neural mechanisms behind social interaction (Oberman, Pineda, & Ramachandran, 2007).

Suppression of the rolandic mu rhythm represents an event-related desynchronization indicated by a reduction in power in the alpha (8-13Hz) frequency band resulting from excitation of the sensorimotor cortex associated with an action (Babiloni et al., 2002; Hari, 2006; Pfurtscheller & Neuper, 1994; Salmelin & Hari, 1994). The mu rhythm suppression is considered to be an index of the hMS because both show similar functional properties, primarily that they both respond not only to the execution of actions but also the observation of an action, and both respond only to goal-directed actions (Le Bel, Pineda, & Sharma, 2009; Oberman et al., 2007; Pineda, 2005). Furthermore, studies measuring functional magnetic resonance imaging (fMRI) and EEG concurrently during action execution and observation tasks demonstrated a close relationship between activity in the hMS and suppression of the mu rhythm (Arnstein, Cui, Keysers, Maurits, & Gazzola, 2011; Braadbaart, Williams, & Waiter, 2013). More specifically, a negative correlation was found between mu power and the BOLD response in putative mirror neuron areas, as a reduction, or suppression in mu power, thus reflecting greater sensorimotor cortical activity. Several studies have shown that the degree of mu rhythm suppression is modulated by the context of the perceived action, not only in terms of visual and spatial properties but also the social context. For example, differences in the orientation of spatial and temporal attention of the observer can modulate the mu suppression, whereby the direction of the spatial attention can have a somatotopic effect (Anderson & Ding, 2011; Ede, Köster, & Maris, 2012; Jones et al., 2010). Some studies have demonstrated that observed actions within a social interactive setting, or even when facial stimuli are directed towards participants, greater mu suppression can be induced, as compared to non-interactive contexts (Ensenberg, Perry, & Aviezer, 2017; Oberman et al., 2007; Perry, Stein, & Bentin, 2011). There is also evidence to show that the intention and social relevance of actions can influence the degree of mu suppression (Kilner, Marchant, & Frith, 2006; Perry, Troje, & Bentin, 2010). The social relationship between observer and performer can also affect activity in this system. One study demonstrated that an action perceived from an interactive partner induced greater mu suppression than actions seen performed by a non-interactive partner (Kourtis, Sebanz, & Knoblich, 2010). Another study found ethnic ingroup / outgroup biases in the mu rhythm, with stronger suppression when observing painful actions from an ingroup member (Riečanský, Paul, Kölble, Stieger, & Lamm, 2015). Furthermore, there is the hypothesis that populations with impairments in social functioning, such as autism spectrum disorders, may also show abnormalities in mu rhythm suppression (Oberman, Ramachandran, & Pineda, 2008). Therefore, it is evident that the mu rhythm likely has some special relevance for social context and social information.

In most social situations in our everyday lives we perform numerous value computations, which in turn, influence our subsequent behavior. Recently, there has been an increasing interest in the interplay between social cognition and decision-making (Frith & Singer, 2008) and particularly, the role of value computations and reward processing in social decision-making (Ruff & Fehr, 2014), which ultimately drive motivated social behaviors and social learning (Heyes, 2012). FMRI studies have found activation in common brain regions during the evaluation of both monetary and social rewards (Izuma, Saito, & Sadato, 2008; Lin, Adolphs, & Rangel, 2012). The striatum, an area central to reward processing and value computation, has consistently been shown to be activated when processing others' rewards and in linking one's own rewards to others' actions (Báez-Mendoza, Harris, & Schultz, 2013). There has been substantial work in patients with Parkinson's disease, a population known to have impairments in theory of mind, suggesting that that the basal ganglia may be involved in social cognition and mirror system activity (Alegre et al., 2010; Alegre, Guridi, & Artieda, 2011; Bodden et al., 2013). Taken together, these studies suggest that some regions central to reward processing are also involved in the integration of social actions and rewards. Further evidence comes from single neuron recordings in area F5 of primate premotor cortex, showing that mirror neurons are sensitive to the value associated with an observed grasping action (Caggiano et al., 2012). Rewards associated with an observed action have also previously been shown to modulate the mu rhythm in humans, whereby actions leading to monetary gains and losses showed greater mu suppression than actions that led to a neutral outcome (Brown, Wiersema, Pourtois, & Brüne, 2013) . Recently, a study confirmed these findings, demonstrating greater mu suppression for face stimuli associated with rewards (Trilla Gros, Panasiti, & Chakrabarti, 2015), further highlighting the influence of rewards on the mu rhythm. In addition to reward valence, affective valence has been shown to affect putative mirror system function in humans, as observed by corticospinal excitability during action observation (Enticott et al., 2012; Hill et al., 2013), as well as more directly in the degree of EEG mu suppression (Moore, Gorodnitsky, &

Pineda, 2012).

In summary, it is clear that the degree of mu rhythm suppression during the observation of others' actions can be modulated by the rewards associated with the seen actions, which has particularly been demonstrated in terms of the valence of rewards and losses. However, the relationship between reward processing and the hMS is still unclear. In addition, it is not clear as to how reward-related modulations in the motor system are specific to rewarding nature of stimuli. More specifically, it is not clear whether the reward-related modulations of the mu rhythm previously seen are driven primarily by reward per se, or by another process associated with rewards. To investigate this further, we developed an action observation paradigm to measure the EEG mu rhythm while participants observed actions that differed in reward valence and magnitude, independently. Our primary aim was to test whether the mu rhythm was affected by both valence and magnitude of rewards associated with the observed actions. As a secondary aim, we wanted to see if this modulation was related to the capacity of relevant social cognitive skills, particularly the ability to understand others' minds (i.e. theory of mind and empathy) and motivated social approach/avoidance behavior. We predicted that both reward valence and magnitude would modulate the degree of mu rhythm suppression during observed actions. More specifically, we hypothesized that we would see a graded effect of reward magnitude and valence, in which the greatest degree of mu suppression would be seen for large rewards, and the least for small losses. We also hypothesized that the degree of overall mu rhythm suppression would be related to theory of mind and empathy, and reward-related modulation of mu suppression would be related more specifically to motivated social approach/avoidance behavior.

2. Methods

2.1. Participants

Twenty-three healthy right-handed students (13 female) were recruited from Uskudar University with a mean age of 22.13 (±2.80; range 20-30), and mean years of education of 14.95 (±0.78). Participants with any history of psychiatric diagnosis or physical health problems that could potentially impair performance on the task were excluded. Everyone had normal or corrected-to-normal vision. All participants also gave written consent to participate, and the study was approved by the local ethics committee.

2.2. Behavioral measures

2.2.1. The Behavioral Inhibition and Activation System Scale (BIS/BAS):

The BIS/BAS self-report questionnaire measures individual differences in two motivational systems that drive behaviors: one being the behavioral approach / activation system (BAS) that regulates appetitive motives to move towards a desired goal, and the other being the behavioral avoidance / inhibition system (BIS), which regulates aversive motives to move away from undesired goals or unpleasant stimuli (Carver & White, 1994). The BIS/BAS consists of 24 items that are answered with a 4-point Likert scale, with answers ranging from '1=very true for me' to '4=very false for me'. Four factor scores are derived from the BIS/BAS scale, including one BIS and three BAS scales: BAS Drive, BAS Fun Seeking, and BAS Reward Responsiveness. It is not recommended to combine the three BAS factors to give one total BAS score.

2.2.2. Reading the Mind in the Eyes Test (RMET):

The RMET is a measure of theory of mind, emotion recognition and the ability to infer others' mental states (Baron-Cohen, Wheelwright, Hill, Raste, & Plumb, 2001). In the test, there are 36 items in which participants are presented with photographs of the eye-regions of individuals along with 4 possible adjectives describing emotional states. Participants are required to choose which emotional adjective corresponds best to the emotion that the person in the photograph is experiencing. Correct responses are summed to give the final score.

2.2.3. The Empathy Quotient (EQ)

The EQ is a self-report measure originally designed to measure multi-dimensional empathy in populations with impairments in social functioning, but is also a suitable measure of temperamental empathy in adults in the general population (Baron-Cohen & Wheelwright, 2004). The test consists of 60 items in which answers range from '1=strongly agree' to '4=strongly disagree'. 40 of these items are summed to give a total EQ score, with the other 20 being filler items. Three factors of the EQ have also been shown to tap into more specific components of empathy, namely cognitive empathy, emotional reactivity and social skills, in which the sums of different groups of questions reveal emotional capacity along these factors (Lawrence, Shaw, Baker, Baron-Cohen, & David, 2004).

2.3. Procedure, task design and stimuli

The action observation EEG task consisted of videos comprising a series of photographs presented sequentially in short succession (~12 frames per second). Each video showed a person (the performer) sitting at a table facing the camera, initially with their hands resting flat on a table. The table had three bowls on it: one in the center closer to the performer, and two others further from the performer, one black and the other white. As the video sequence began, the performer reached into the bowl closest to them, took out a colored coin that was either red or green, and placed it into one of the two other bowls. The performer then returned their hands back to the original resting position. Each trial consisted of one video in which either a red or green coin was taken from the center bowl and placed into one of the other two bowls. A red coin always represented a loss and a green coin always represented a win. Performers' faces were not included in the stimuli in order to try to control for possible confounding effects, such as ingroup and outgroup preferences. One trial lasted for a total of 4500ms, with the observed action lasting 2000ms, followed by a 2500ms inter-stimulus interval in which the performer was seen sitting still in the resting position. One short practice block consisting of 8 trials was completed before the main experimental blocks. Two sets of three blocks of 50 trials each made up the experiment, which comprised a total of 300 trials. In one version of the experiment, for the first three blocks of trials coins only went into the white bowl, whereby red coins represented a small (-10 cents) loss and green coins representing a small win (+10 cents). In this version, for the second set of three blocks of trials, each coin represented big losses (-100 cents) and wins (+100 cents). Another version of the experiment presented the converse, i.e. big wins and losses in the first three blocks of trials, and small wins and losses in the second set of three blocks of trials. These two versions of the experiment were counterbalanced across participants.

Throughout the EEG experiment, participants were seated in front of the computer screen that was presenting stimuli, with their hands resting flat on the table. All participants were clearly instructed to stay as still as possible and to only keep in mind the cumulative amount they won in each block. At the start of each block, participants were told that they would start with 100 cents (for all blocks and conditions) and that the money will be added up at the end of the experiment. The experimenter recorded the amount participants had counted at the end of each block. This was done to ensure that participants were paying attention to wins and losses during each trial. Figure 1 illustrates the experimental task design, with example screenshots of stimuli.

2.4. EEG data acquisition and analysis

EEG activity was recorded at a sampling rate of 1000 Hz (Pycorder 1.9) using a Brain Products actiCHamp 32 channel system with active electrodes (Brain Products, Munich, Germany). Electrodes were positioned on the participant's heads according to the international 10-20 system, held in place by an elasticated electrode cap, with the reference and ground electrodes between Fz and Cz, and between FC1 and FC2, respectively. Horizontal eye movements were recorded by bilaterally electro-oculogram (EOG) electrodes placed at the outer canthi of both eyes. All electrode impedances were kept below 10 kΩ.

Preprocessing of EEG data was done offline using the BrainVision Analyzer software package (Brain Products, Munich, Germany). All data was first down-sampled from 1000Hz to 500Hz, and then re-referenced to the linked mastoids, and a high-pass filter of 0.1Hz, with a 50Hz notch filter applied. Ocular correction was done using an independent component analysis method (Jung et al., 2000). The 2000ms action epoch was segmented into 1000ms epochs and averaged for each condition (small win, small loss, big win, big loss), and these 1000ms epochs were then used as the main action epochs for further analysis. Movement artifacts were identified with criteria that rejected signal gradients greater than 50μV, or epochs where signal exceeded -300μV or 300μV, which resulted in ~5% of the data being removed. For the baseline epoch, the 1000ms preceding the onset of the action was taken and averaged across conditions. Baseline epochs were submitted to the same artifact

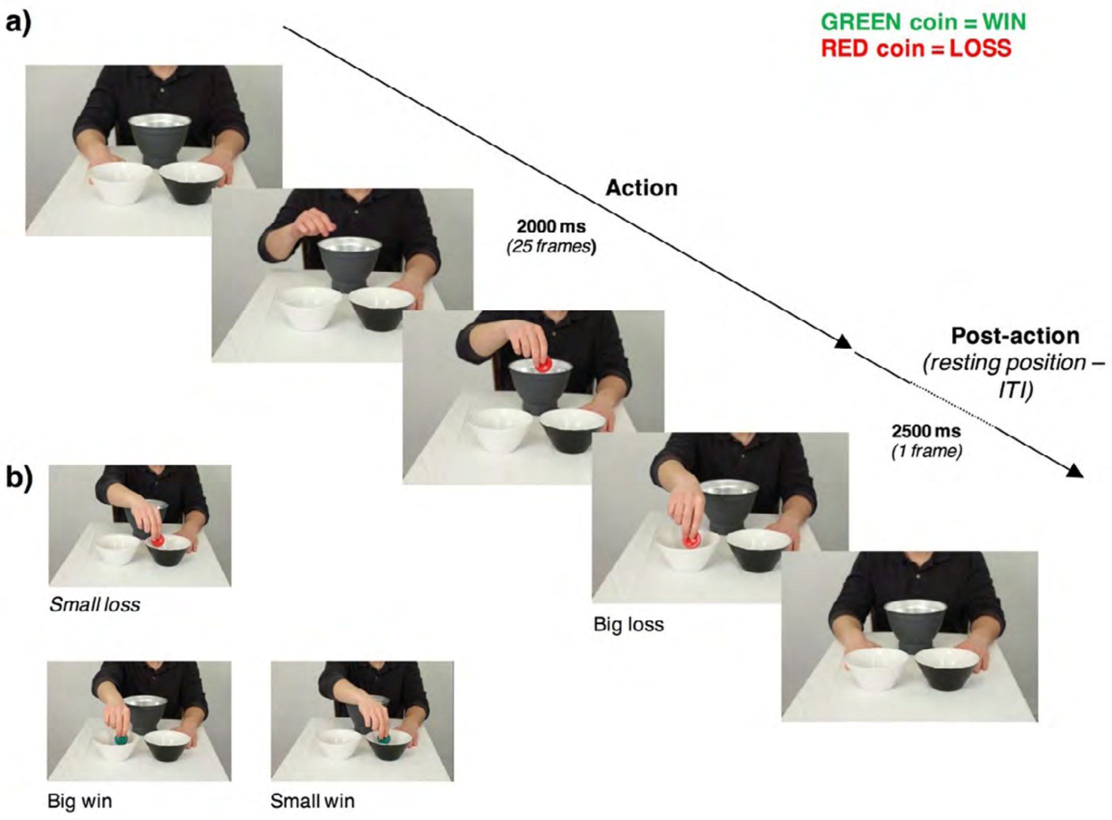

Figure 1. EEG experimental task design

rejection procedure. A Fast Fourier Transform (FFT) was performed on each of the 1000ms epochs and an average was then taken for each condition, and power values in the alpha frequency band (8-13Hz) were extracted.

Following previous studies, we determined mu suppression by calculating event-related desynchronization / synchronization (ERD/ERS) for central electrodes overlaying sensorimotor cortex (C3, Cz and C4) using the standard formula: [(alpha power during action epoch – alpha power during baseline) / alpha power during baseline) x 100] (Pfurtscheller & Neuper, 1994).

2.5. Statistical analysis

To investigate relationships between the behavioral measures, we performed a Pearson's correlation analysis with all scales and subscales of behavioral data collected.

For the EEG data, to test for effects of reward magnitude and valence on the mu rhythm, a repeated-measures ANOVA was performed using the mu rhythm suppression values for reward magnitude conditions (large, small), reward valence conditions (win, loss) and electrode positions (C3, Cz and C4) as within-subject factors. Post-hoc comparisons were conducted for significant main effects. In order to check for the regional specificity of significant effects, relevant post-hoc statistical tests were also performed on the frontal, parietal, and occipital electrodes that spanned the midline (F3, Fz, F4; P3, Pz, P4; O1, Oz, O2). Several studies have shown that age and sex are related to the degree of mu rhythm suppression (Cheng et al., 2008; Marshall, Bar-Haim, & Fox, 2002), therefore a further ANCOVA was performed to verify reward-related effects after covarying out the influence of age and sex.

In order to investigate relationships between the mu rhythm differences in response to reward valence / magnitude and behavioral measures, we calculated mu reward valence and reward magnitude effect scores. This was done by subtracting the mu rhythm for large wins / losses from small wins / losses (reward magnitude mu effect), and all wins subtracted from all losses (reward valence mu effect). Reward valence and reward magnitude mu effects were calculated for each individual to reflect the relative differences and individual variability in mu power between reward valence and magnitude conditions. Pearson correlation analyses were performed with behavioral scores and reward magnitude and valence mu effect scores. Furthermore, to control for the potential influence of age and sex, a partial correlation analysis was also done with significant correlations to further confirm significant relationships.

3. Results

Table 1 shows means and standard deviations for demographic data and scores on measures of social cognition.

3.1. EEG mu rhythm suppression

The results of the repeated-measures ANOVA revealed a main effect of reward valence (i.e. wins and losses), (F(1, 22)=7.260, p=0.013, ηp2=0.248). However, no other main effects or interactions were found in any other factors (all p>0.05). Post-hoc comparisons showed significantly greater mu rhythm suppression for losses, compared to wins when pooling mu suppression values over central electrodes and reward magnitude conditions (t=2.694, p=0.013). Importantly, post-hoc comparisons for wins and losses over other regions showed that there were no significant differences over frontal, parietal or occipital areas (all p>0.05). Figure 2 shows mu rhythm suppression for wins and losses pooled over central electrodes.

Tablo 1. Demographics showing means and standard deviations (SD) for participants.

	Mean	SD
Age	22.13	2.80
Sex	10M / 13F	-
Education (yrs)	14.95	0.78
BIS	20.13	4.34
BAS reward	17.83	2.76
BAS fun	13.30	2.51
BAS drive	11.70	3.23
RMET	23.22	3.33
EQ total	25.78	13.04
EQ cog empathy	12.65	7.20
EQ emotional react	12.83	4.51
EQ social skills	6.30	2.88

Notes: M = male, F = female; BIS = Behavioral Inhibition System scale; BAS = Behavioral Activation System scale; RMET = Reading The Mind in the Eyes Test; EQ = Empathy quotient (3 factors; cognitive empathy, emotional reactivity, social skills).

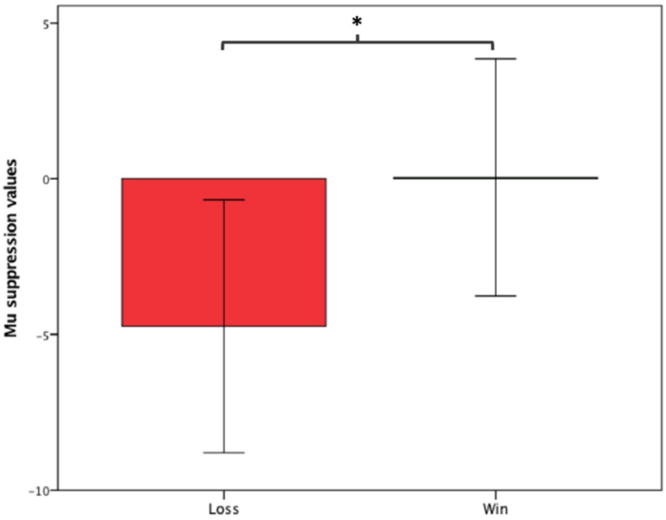

Figure 2. Bar chart showing percentage change in mu rhythm power for wins and losses during the action observation task, relative to baseline. Error bars represent one standard error of the mean (*p<0.05)

After controlling for age and sex as covariates with an ANCOVA with mu suppression values, the main effect of reward valence remained (F(1, 20)=7.425, p=0.013, ηp2=0.271). As expected, we additionally saw a significant interaction between reward valence and age (F(1, 20)=6.285, p=0.021, p=, ηp2=0.239). No other main effects or interactions were significant (all p>0.05).

3.2. Relationship between mu suppression and behavioral data

Due to the significant main effect of reward valence, but a lack of effects for other conditions, mu rhythm values were pooled across reward magnitude conditions and electrodes, and only the reward valence mu effect was used for the correlation analysis with demographic variables and social cognition measures.

In line with the results from our ANCOVA analysis, we see a significant negative correlation between age and the reward valence mu effect (r=-0.443, p=0.034) whereby the effect of reward valence on the mu rhythm was less for older participants.

Most interestingly, we see a strong positive correlation between the reward valence mu effect and empathy as measured by the total EQ score (r=0.731, p<0.001). A scatterplot for this relationship is shown in figure 3. After controlling for age, the correlations between the reward valence mu effect and EQ scores remained significant, and even became stronger (r=0.806, p<0.001). In addition, significant correlations were found between the mu reward valance effect and the cognitive empathy (r=0.433, p=0.039) and emotional reactivity (r=0.693, p<0.001) factors of the EQ, but not with the social skills factor of the EQ (r=0.164, p=0.454). The correlations with cognitive empathy (r=0.641, p=0.001) and emotional reactivity (r=0.712, p<0.001) also remained significant after controlling for age. There were no other significant correlations between the reward valence mu effect and other behavioral measures. Importantly, there were also no other significant correlations between the mean mu rhythm values (pooled over all electrodes, reward magnitude and reward valence conditions) and any behavioral measures (all p>0.05).

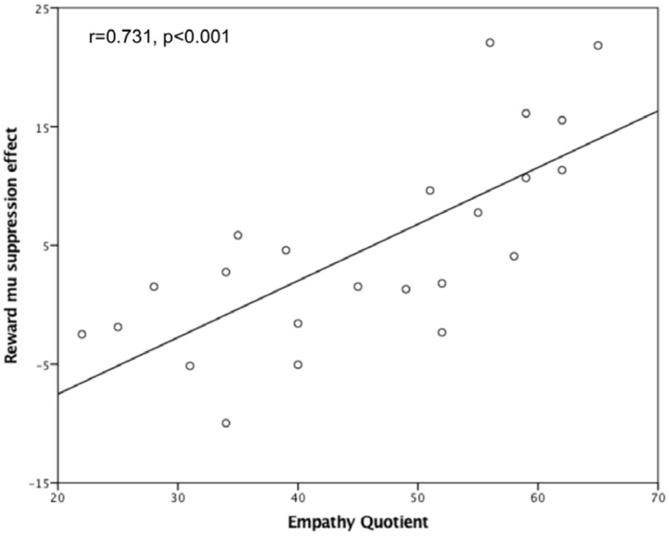

Figure 3. Scatterplot showing the relationship between the reward-valence mu rhythm effect (i.e. difference between wins and losses) and total scores on the Empathy Quotient.

4. Discussion

In this study, we sought to investigate the effects of reward valence and magnitude on the degree of EEG mu rhythm suppression during an action observation task in which the observed actions led to rewarding or loss outcomes of different financial values. As a secondary aim, we asked the question of whether the effect of rewards on the mu rhythm were related to demographic and social cognition variables, including age, motivated social approach/avoidance behavior, theory of mind and empathy. We showed that the mu rhythm was modulated by reward valence, but in the opposite direction to which we hypothesized, whereby greater mu rhythm suppression was evoked by action outcomes associated with losses, when compared to action outcomes associated with rewards. We demonstrated that this effect could not be accounted for by differences in age or sex. However, contrary to our hypothesis, we did not see any effect of reward magnitude on the degree of mu suppression. Interestingly, the effect of reward valence on the mu suppression correlated with levels of empathy, in which people with more empathy exhibited a greater reward valence mu suppression effect. Furthermore, the relationship between the effect of reward valence on the mu suppression and empathy was specific to cognitive empathy and emotional reactivity, but not social skills nor affective theory of mind. To our knowledge, this is the first study demonstrating a specific effect of reward valence on the mu rhythm, and not magnitude, and the first to show that this reward-related modulation was associated with levels of cognitive empathy and emotional reactivity.

Our main findings provide further evidence to support the role of reward processing in the mirror motor system, particularly during the observation of others' actions, which has previously been suggested by other mu rhythm studies (Brown et al., 2013; Brown, Gonzalez-Liencres, Tas, & Brüne, 2016) . The greater mu rhythm suppression in response to losses was in contrast to what we had hypothesized, as we had predicted that greater suppression would be seen for wins overall. Other studies from our group have shown some divergence in the direction of the mu rhythm change in response to monetary wins and losses using a similar paradigm (Brown et al., 2016), where we have found greater mu suppression for relative losses, compared to winning and neutral actions. This suggests that the link between rewards and the mirror system may not be as straightforward as we had expected. There has been some work investigating the influence of affective valence on motor cortex excitability, though it did not directly address reward processing. One such study by Hajcak et al. (Hajcak et al., 2007) used transcranial magnetic stimulation (TMS) to demonstrate that the magnitude of motor evoked potentials (MEPs) were greater when presenting participants with pleasant or unpleasant images, when compared to neutral images. Other more recent studies have also shown this bidirectional relationship with both positive and negative emotions increasing activity in the motor system (Hill et al., 2013). In contrast, there is also evidence showing that negatively valenced stimuli evoked greater motor-related corticospinal excitability when compared to positively valenced stimuli (Enticott et al., 2012; Anaelli

A. Nogueira-Campos et al., 2016; Anaelli Aparecida Nogueira-Campos et al., 2014). The mixed results from these previous findings, and the possible bidirectional relationship between positive and negative emotions and possible modulations on the mu rhythm may depend upon individual differences in emotional processing and empathetic responses, especially as our findings show a relationship between empathetic capacity and the degree of reward-related mu suppression. Taken together, it is evident that both reward valence and affective valence have a role in the processing of one's own and of others' actions, which could shape motivational drives and thus influence our behaviors in social contexts.

One interpretation of our results is that the reward valence modulation of the mu suppression may be driven by salience, which could be a product of the subjective experiences of monetary losses or gains. The suggestion that salience drives our main findings may be supported by the correlation we see between emotional reactivity and the reward valence mu effect. In the reward processing literature, it is currently accepted that there are two motivational systems that drive reinforcement-learning processes, namely 'liking' and 'wanting' (Berridge, 2007). As no learning was involved in our paradigm, our results may speak more to the 'liking' dimension of reward processing, which represents the hedonic impact of the receipt of rewards, whereas the dopamine-mediated 'wanting' dimension induces incentive salience, which drives goal-directed behaviors to seek rewards. However, one very elegant study using a Pavlovian-to-Instrumental paradigm with real-time fMRI found enhanced responses in motivational areas including ventral striatum and amygdala upon presentation of reward-related cues during motor imagery (Mendelsohn, Pine, & Schiller, 2014). The authors highlight work showing the importance of ventral striatum and amygdala in signaling the incentive value of stimuli (Berridge, Robinson, & Aldridge, 2009; Everitt, Cardinal, Parkinson, & Robbins, 2003), and thus conclude that their results demonstrate a concurrent activation of the 'value' and 'action' networks. Additionally, Klein-Flugge et al. (Klein-Flügge, Kennerley, Friston, & Bestmann, 2016) demonstrated activation in a network that encompassed the dorsal anterior cingulate cortex (dACC) and supplementary motor area during both a reward value comparison task and an effort-discounting task. As we know that mu suppression is evoked by motor imagery (Pfurtscheller, Brunner, Schlögl, & Lopes da Silva, 2006), taking these findings into consideration, it would be reasonable to suggest that the reward-related mu rhythm effects we see in our study may also be representative not only of the experience of reward receipt, but also of the differences in reward valuation, especially as high and low rewards are presented relative to each other. There is also other evidence from patients with Parkinson's disease where authors have suggested a link between the reward circuit of the basal ganglia and the human mirror system (Alegre et al., 2010; Alegre et al., 2011). It is difficult to disentangle salience from the hedonic experience of rewards, although future studies could seek to integrate conditions of positively and negatively valenced salience and gains and losses of rewards in combination to compare the magnitude of these effects on mu suppression. Measuring emotional reactivity in future studies could also provide more insight into the possibility that salience could be contributing to the reward-related modulation of the mu rhythm. Future studies using combined EEG and fMRI with reinforcement-learning paradigms could also help to determine whether the reward-related modulation we see in the mu suppression also extends to the learning and 'wanting' aspects of reward processing.

The relationship we see between empathy and the mu suppression effect is supported by other studies, which have consistently demonstrated a generalized relationship between activity in the mirror system and trait levels of empathy (Cheng et al., 2008; Pfeifer, Iacoboni, Mazziotta, & Dapretto, 2008; Schulte-Rüther, Markowitsch, Fink, & Piefke, 2007; Yang, Decety, Lee, Chen, & Cheng, 2009). However, none of those studies have characterized this relationship specifically in terms of reward-related mu rhythm modulation. There is some evidence to suggest a relationship between empathetic capacity and a vicarious reward prediction error signal in the ACC when observing others' receiving a reward (Lockwood, Apps, Roiser, & Viding, 2015). The fMRI study from Lockwood et al. (2015) found that activation in the anterior cingulate cortex (ACC) in participants with less empathy corresponded to receipt of rewards for the self and others, whereas ACC activation in those with high trait empathy was related only to others' rewards. Interestingly, one study investigating the kinematic response during the simulation of feeding others in various emotional contexts found different kinematic profiles depending on the emotions expressed by the actors being fed (Ferri et al., 2010). These salience-driven effects on the motor system were modulated by the participants' empathetic attitudes, supporting our findings with regards to the relationship between individual differences in empathy and action processing in a social setting. It is important to note here, that one possible reason for not seeing a correlation with the other behavioral measures was because of their low variance. It seems that the empathy score was the only measure in which there was substantial variance between participants. Our results add to the literature by suggesting that the influence of trait empathy on social action processing also extends to reward valuation in the mirror system.

There were some unexpected findings in our study, some of which have already been discussed. A main finding that was contrary to our hypothesis was the lack of reward magnitude effects on the degree of mu suppression. One explanation for this may be due to our design and the distribution of our experimental conditions in trials and blocks. The conditions of reward magnitude were presented across different blocks of trials, whereas different reward valences were presented within each block. In other words, the relative comparisons of reward magnitude were more separated in time than comparisons of reward valence. Therefore, the relative difference between high and low reward magnitudes may have been less salient than the relative difference between wins and losses, resulting in the effect of reward valence overshadowing the relative response to differences in magnitude. This issue of the relativity between conditions may have also accounted for the unexpected finding of a small mu suppression for wins, relative to losses. Due to the fact that we did not have a neutral condition, the trials that led to a win may have evoked a mu rhythm response that was relatively neutral when compared to a loss, which appeared to be more salient. Having a mixed design rather than the block design used here, may have made the relative effects of the reward conditions more balanced.

There were a number of limitations to our study, one of which was our lack of a neutral condition in which participants experienced neither reward nor loss. As already mentioned, this makes it hard for us to draw strong conclusions about the relative effects of high and low rewards and losses on mu suppression. Furthermore, there was no visual difference between small and large wins and losses, which may have dampened potential reward magnitude effects. Future studies may wish to make more distinct visual differences across conditions, and may also consider using a mixed block design to enhance possible reward magnitude effects. Another limitation of this study was due to the inherent lack of spatial resolution in EEG, which makes it difficult to make inferences about the source of the reward-related modulation of the mu suppression. Using a combination of fMRI and EEG to utilize both high spatial and temporal resolution in future studies would provide further insight into the source of this effect, alternatively, independent component analysis and dipole fitting could be used with EEG alone to localize the source of the signal. As already mentioned, the reward-related modulation may have been driven by salience, and so a final limitation of the study was that no behavioral measures related to individual differences in trait salience processing were collected.

This study is the first to demonstrate that the reward-related modulation of the human mirror system, as indexed by the mu rhythm suppression, is specific to reward valence but not reward magnitude. Furthermore, we reveal a novel relationship between the effect of reward on the human mirror system and trait empathy. We conclude that the mirror system may be sensitive to reward value encoding, which could be related to salience processing. In the larger context of social decision-making, the subjective value and salience we associate with social stimuli is likely to play a central role in what we attend to, and are drawn towards. Thus, value may shape the degree to which we engage in social interactions, as well as influencing from who, what and where we learn our social skills, and could guide the choices we make in our social lives.

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