Integration of action value during action observation

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Abstract

Transcranial magnetic stimulation (TMS) studies consistently demonstrated that observing the actions of other individuals leads to a muscle-specific increase in primary motor cortex (M1) excitability (i.e., motor resonance). Although it has been shown that motor resonance is modulated by contextual information accompanying others' actions, it is currently unknown whether action value is integrated into behavioral and physiological outcomes during action observation.

Here, we tested whether response times (RT; experiment 1) and muscle-specific motor resonance (experiment 2) are modulated by the value associated with an observed action. Our results show that observing highly-valued actions leads to a decrease in RT variability, as well as a strengthening of muscle-specific motor resonance. This sharpening of behavioural and neural responses was contrasted to a matched control task that manipulated attention independent of the reward value. Collectively, our findings suggest that action value is integrated during action observation and is able to enhance both the precision of behavioral responses, as well as the neural tuning of M1 action representations.

1. Introduction

Observing the movements performed by another individual automatically triggers motor resonance (i.e., increased corticospinal excitability) in the primary motor cortex (M1). This propagates to primary motor cortex (M1) and is thought to be mediated by the mirror neuron system (MNS) (for a review, see Naish et al., 2014). M1 activity during action observation can be modulated by higher-order information, such as the context in which the action is taking place (Amoruso & Urgesi, 2016), characteristics of the agent performing the action (Bunday, Lemon, Kilner, Davare, & Orban, 2016) or moral connotations of observed actions (Craighero & Mele, 2018). Yet, the contribution of action value (i.e., reward associated with observed actions) to M1 motor resonance in humans has remained unclear.

The only direct evidence for the influence of reward on the MNS activity comes from a recent study in primates (Caggiano et al., 2012). Caggiano and colleagues identified mirror neurons in area F5 of the monkey premotor cortex which were modulated by the subjective value associated with the observed actions. They showed that neural firing of grasp-specific mirror neurons was modulated by whether the grasped object was rewarding or non-rewarding. While most neurons fired when the subjective reward value of the object grasped by another agent was high, some had a preference for less-relished or no rewards. Thus, the observer's subjective value associated with the to-be-grasped object modulated how the observed action was represented by mirror neuron activity. The authors argued that this effect was observed over and above potential attention-related responses.

In humans, the existence of a similar interaction between subjective value representations and motor resonance (i.e. brain activity reflecting observed motor actions), can only be drawn on the basis of indirect evidence. Previous studies proposed that electrophysiological markers of motor resonance (i.e., decreased power in mu band measured with electroencephalography (EEG)) are modulated by the observation of rewarding stimuli (Brown, Gonzalez-Liencres, Tas, & Brüne, 2016; Brown, Wiersema, Pourtois, & Brüne, 2013; Trilla Gros, Panasiti, & Chakrabarti, 2015). In particular, they found more pronounced mu suppression (interpreted as stronger motor resonance) when observing rewarding actions which suggests that the higher subjective value of an observed action, the stronger is the response of the observers' sensorimotor system.

Here we aim to further unravel how subjective value influences motor resonance in humans and, specifically, whether it affects the grasp-specific tuning of neural activity in the observer's brain. To do so either a precision grip or a whole hand grip was associated with high versus low reward. We first asked whether the value an observer associates with another persons' actions has any implications for behavioral readouts. We found that a high subjective value increased the precision of the observer's responses, an effect that was present over and above the influence of attention. Second, we tested whether reward influences the action specific tuning of neural activity in primary motor cortex when precision versus whole-hand grasps were observed under rewarded versus non-rewarded conditions. This was indeed the case and action-specific motor resonance in M1 was modulated significantly stronger by reward than by attention alone.

Thus, our results suggest that high reward value associated with an observed action leads to more precise behavioural responses and sharper grip-specific tuning of neural representations which could potentially be driven by an improvement of the signal-to-noise ratio of task-relevant characteristics.

2. Materials and Methods

In two separate experiments, we examined whether reaction times (experiment 1) and muscle-specific motor resonance (experiment 2) are modulated by the value associated with an observed action. Both involved participants viewing grasping movements presented on a computer screen. Further details regarding the movement stimuli are presented in the section below, followed by information specific to each experiment.

2.1. Movement stimuli

In both experiments, participants observed either a precision-grip (PG) or a whole-hand grip (WHG). These actions were presented in an implied motion paradigm (still shots of two different grasping movements; **Figure 1**). We chose to show static images presented in succession to give the impression

of movement rather than complete action videos in order to have more control over the timing of the sequence of events. Stimuli were created by showing a series of three still shots from videos of a hand reaching, grasping and lifting a round jar (9 cm diameter, 14.5 cm height, 1.5 kg weight). These still shots were chosen from videos that were used previously (Cretu, Ruddy, Germann, & Wenderoth, 2019; de Beukelaar, Alaerts, Swinnen, & Wenderoth, 2016). In WHG all fingers were used to grasp the lid of the jar, whereas for the PG, only the thumb and index finger grasped a small knob mounted on the top of the jar. Each trial started with a fixation cross which stayed on the screen for a random duration between 3.5 and 4.5 seconds followed by the reach, grasp and lift pictures – each remaining visible for 0.6 seconds. In the reach picture, the jar was visible in the middle of the screen together with the right hand of an actor positioned in the upper right corner as a clenched fist. Importantly, both WHG and PG condition were identical at this phase. The grip type only became apparent in the second and third pictures which showed the hand grasping the jar and lifting it approximately 15 cm above the surface. The occurrence of WHG and PG trials was randomized to avoid anticipation on the type of grasp.

Depending on the experiment, we either recorded response-times (RTs; experiment 1) or motor-evoked potentials (MEPs; experiment 2) during the grasping snapshot.

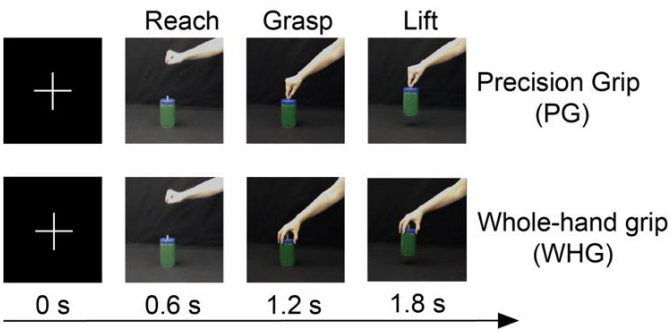

Figure 1 Movement stimuli

Schematic representation of a precision grip (PG) and a whole-hand grip (WHG) trial structure. A fixation cross was presented for a random duration (3.5 – 4.5 seconds) followed by the reach, grasp and lift still shots (0.6 seconds each). During the experiment, PG and WHG trials were randomly intermixed.

Reward condition and counting control

Both experiments employed two main conditions: a **reward** condition and a **counting** control condition. Additionally, in each block, one of the two graps types was task-relevant (i.e., the **target**) while the other was task-irrelevant (i.e., the **non-target**). In the reward condition, subjects had to count the accumulated monetary reward directly associated with the target, while in the counting condition, they had to count how many times they saw the target.

2.2. Experiment 1: behavioral effects of reward during action observation

2.2.1. Participants

49 volunteers were recruited for this experiment. Of these, two were excluded from the final analyses because of their high rate of wrong button presses (i.e., button presses in more than 10% non-target trials). Thus, the final sample for this study included 47 participants (25 women, mean age ± sd 27.25 ± 6.73 years old, right-handed). All experimental protocols were approved by the research ethics committee of the canton of Zurich (no. 2017-01001). Participants gave informed consent to the study, were paid for participation and received a random cash bonus which depended on their performance during the experiment (max. 20 Swiss francs; for more information see the *Behavioral paradigm* section).

2.2.2. Behavioral paradigm

In this experiment, we assessed the behavioral effects of reward during action observation by analyzing response times. Each trial always started with a fixation cross which stayed on the screen for a random duration between 3.5 and 4.5 seconds followed by the reach, grasp and lift pictures – each remaining visible for 0.6 seconds. The occurrence of WHG and PG trials was randomized to avoid anticipation on the type of grasp.

Participants had to perform 18 blocks each consisting of 16 trials (on average: 50% PG and 50% WHG). Prior to each block they were instructed to attend to one of the grasp types (i.e., the target) while the other was task-irrelevant (i.e., the non-target). Importantly, one of three different values could be assigned to the target action: 2 Swiss francs (i.e., high reward blocks, n=6), 0.02 Swiss francs (i.e., low reward blocks, n=6) or 0 Swiss francs (i.e., counting control blocks, n=6), as it can be seen in **Figure 2** below. Participants pressed a button whenever they saw the target action (PG or WHG, depending on the block). In reward blocks, subjects had to additionally count the accumulated reward associated with the target grasp. After the button press was recorded, the respective monetary reward was shown as a coin appearing during the lifting snapshot to remind participants that this is the task-relevant target grasp and whether they could earn a low or high reward. After each block, the accumulated sum of reward was written down and the participants were informed that only the *correct* sum is considered for renumeration (see below).The counting control blocks followed a similar structure. The main difference was that participants had to simply count how many times they saw the target grasp . After each block, the count of the target action was written down and the participants were informed that only the *correct* count is considered for renumeration (see below). All tasks required the same simple button press (i.e., spacebar) to ensure that any resulting differences in reaction time across these blocks were

dependent only on the reward expectancy (i.e., high vs. low reward vs. count), and not driven by differences in task difficulty. Thus, depending on the block instructions, we either investigated reward effects (target action is rewarded) or attentional effects (target action is counted).

Prior to the experiment, participants were informed about our renumeration scheme which incentivised them to have a good performance throughout the whole duration of the experiment. In particular, participants were instructed that only one block will be picked randomly and remunerated at the end of the experiment. If a reward block was chosen, the amount of money depended on the total sum accumulated in the block but only when this sum was reported correctly. If a counting block was chosen, participants were informed that although no value is directly associated with the target grasp, a fixed reward was offered if the reported count was correct. This payoff structure ensures that subjects are motivated to attend to the target grasp independent of the block type.

Feedback was never given on a trial-by-trial basis since this might lead to reduced task-performance (Kluger & Denisi, 1996) and unwanted trial-by-trial dynamics. However, feedback was given at the end of each block. Subjects only had to press a button for the target grasps. In total, 24 RTs were recorded for each of six experimental conditions, i.e. 2 grip types (WHG, PG) x 3 tasks (low reward, high reward count), resulting in a total of 144 RTs for each subject.

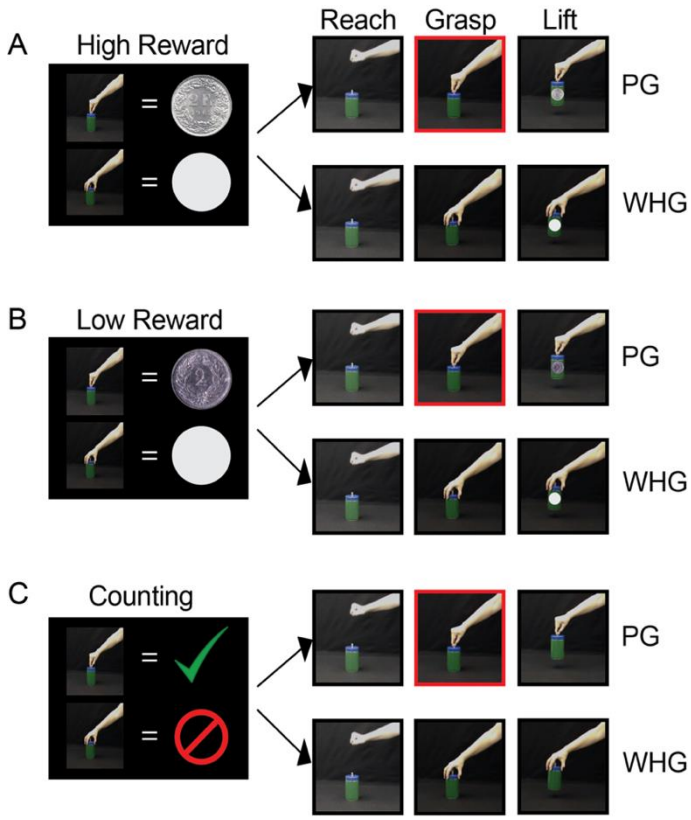

Figure 2 Illustration of behavioral task instructions and trial structure

All examples depict blocks in which precision grip (PG) is the target and whole-hand grip (WHG) is the non-target action. The red frame indicates the snapshot in which the response times were recorded. (A) High reward block: 2 Swiss francs associated with the target. (B) Low reward block: 0.02 Swiss francs associated with the target. (C) Counting attentional block: no monetary reward associated with the target.

2.2.3. Behavioral analysis

Response time (RT) was the primary outcome variable of this experiment and was defined as the time between grasp snapshot onset and the button press. Occurrences of unusually quick responses (faster than possible to recognize the target grasp and perform a motor response; i.e., 200 ms) were removed from the analyses (0.76 % of all trials). This criterion was chosen based on previous research indicated that muscle-specific increases in corticospinal excitability should be visible from around 200ms post-onset (Naish et al., 2014). Subjects only had a short time window of 600ms to respond to the target grasp and if they were too slow to respond in that time window, it counted as a miss (0.2 % of all trials).

An Ex-Gaussian model was fitted to the remaining RT data for each condition and subject and three model parameters (mu, sigma, and tau) were estimated using the Matlab toolbox exgauss (Zandbelt, 2014). The advantage of ex-gaussian fitting is that the positive skewness of response time distributions is considered by combining a normal Gaussian distribution with an exponential component. This form of fitting has been extensively used in the literature (a few examples: Balerna & Ghosh, 2018; Tarantino, Cutini, Mogentale, & Bisiacchi, 2013; Tschentscher & Hauk, 2014). The mu and sigma parameters reflect the mean and standard deviation (sd) of the gaussian component of the RT distribution while tau describes the exponential distribution (Lacouture, 2008).

Data points of subjects that were less or greater than Q1-1.5*IQR or Q3+1.5*IQR respectively (Q1, first quartile; Q3, third quartile; IQR, Interquartile Range), were considered as outliers and therefore, rejected from the analysis (n = 5). To investigate the effects of observed action value (low, high reward or count) on behavioral performance, mean response time and ex-Gaussian parameters (mu, sigma, tau) were analyzed using RM-ANOVA. Error rates were analysed in the same manner.

Counting errors (i.e., wrong count of the accumulated reward or count) as well as incorrect, early and late button presses (i.e., button presses during non-target grasps, during reach or lift respectively) were inspected to ensure that cognitive demand was comparable across the three experimental tasks (i.e., low, high reward or counting).

2.2.4. Statistical analysis

Statistical analyses were performed using repeated-measures analysis of variance (RM-ANOVA) in JASP (Version 0.8.5.1, https://jasp-stats.org/). Estimates of the effect sizes are reported in the tables using partial eta squared (small $\eta_p^2 = 0.01$, medium $\eta_p^2 = 0.06$, large $\eta_p^2 = 0.14$; Lakens & Bakker, 2013). The significance threshold alpha=.05 was chosen for all statistical tests and FDR corrections for multiple comparisons were applied when necessary. Results are reported in the figures as mean ± standard error of the mean (SEM). Additionally, we added estimation plots to depict Cohen's d effect

sizes (small d = 0.20–0.49, medium d = 0.50–0.80, large d > 0.80; Cohen, 1988) and their confidence intervals in form of bootstrap sampling distributions using open-source code (*www.estimationstats.com;* Ho, Tumkaya, Aryal, Choi, & Claridge-Chang, 2019).

2.3. Experiment 2: Transcranial Magnetic Stimulation Experiment

2.3.1. Participants

34 volunteers were recruited for a transcranial magnetic stimulation (TMS) experiment (19 women, mean age ± sd 25.8 ± 4.8 years old). All subjects were right-handed, as assessed with the Edinburgh Handedness Questionnaire (Oldfield, 1971), naive about the purpose of the experiment and had normal or corrected-to-normal vision. All participants were screened for potential contraindications to brain stimulation (Rossi et al., 2009) and written informed consent was obtained before starting the task. Subjects were paid for participation but additionally received a random cash bonus which depended on their performance during the experiment (max. 20 Swiss francs; more information in the *Behavioral paradigm* section). Additionally, the experiments were approved by the research ethics committee of the canton of Zurich (no. 2017-01001).

2.3.2. Behavioral paradigm

The goal of this experiment was to test the effects of reward on action-specific responses elicited during action observation. The task design was the same as in Experiment 1, except for the following two changes. First, participants were instructed to be as relaxed as possible during the task and simply count either the accumulated reward or the number of target grasps (i.e., no button press required during the grasp presentation). Second, in the reward blocks, in order to ensure that subjects focused on the value of the action and did not simply count the target grasps, we showed either 1 or 2 Swiss francs coins during the lifting phase randomly interleaved within a block which they had to sum up and report at the end of each block (**Figure 3**). For non-target trials, a coin-like circle appeared in the same location and at the same time point.

The payoff structure was similar to the one presented in Experiment 1. Namely, one random block was picked and remunerated at the end of the experiment, if subjects performed the task correctly. The amount of money corresponded to the sum accumulated in the respective block (reward condition) or was a fixed sum which was given for good performance (i.e., correct counting; count condition)

TMS single-pulses were sent after 250 ms from the presentation of the grasp snapshot. Previous electrophysiological and TMS research showed that motor resonance can be observed around 250 ms after action onset (Barchiesi & Cattaneo, 2013; Cavallo, Heyes, Becchio, Bird, & Catmur, 2014; Ubaldi, Barchiesi, & Cattaneo, 2015; C. Urgesi, Moro, Candidi, & Aglioti, 2006; Cosimo Urgesi et al., 2010).

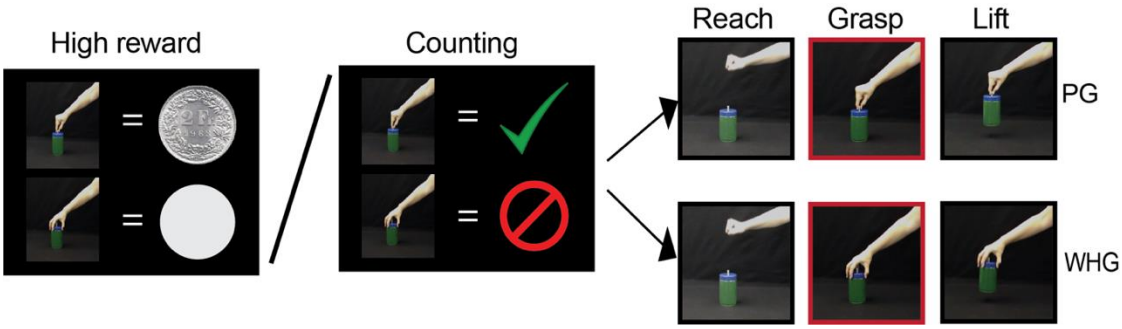

Figure 3 Illustration of TMS task instructions and trial structure

Schematic representation of the TMS task instructions and examples of precision grip (PG) and whole-hand grip (WHG) trials. Instructions depict a high reward and a counting block in which PG is the target and WHG is the non-target action. The red frame indicates the snapshot in which the TMS pulses were sent and motor – evoked potentials were recorded.

Here, for each of the eight conditions [2 grip types (WHG, PG) x 2 target types (target, non-target) x 2 tasks (reward, count)], 24 MEPs were recorded, resulting in a total of 192 MEPs for each subject and each muscle (FDI, ADM).

2.3.3. Electromyographic recordings and TMS procedure

Corticomotor excitability was measured using TMS and motor-evoked potentials (MEPs) were simultaneously recorded from the First Dorsal Interosseous (FDI) and Abductor Digiti Minimi (ADM) of the right-hand using surface electromyography (EMG; Delsys Bagnoli DE-2.1). EMG data were recorded using Signal Software (Version 5.07, Cambridge Electronic Design, UK), sampled at 5000 Hz (CED Power 1401; Cambridge Electronic Design, UK), amplified, band-pass filtered (30–1000 Hz), and stored on a PC for off-line analysis. TMS was performed by means of a 70 mm figure of eight coil connected to a Magstim200 stimulator (Magstim, Whitland, UK). Since we wanted to make sure that MEPs are consistently elicited in both muscles, we defined the optimal scalp position (hotspot) as the position from which stable responses were simultaneously evoked in both the right FDI and ADM muscles. The resting motor threshold (rMT) was defined as the lowest stimulus intensity evoking MEPs in the right FDI and ADM with an amplitude of at least 50 µV in 5 out of 10 consecutive stimuli (Rossini et al., 2015). Subjects' rMT, expressed as a percentage of the maximum stimulator output, was on average 45 % (range: 34% - 57%). TMS triggering was controlled using Matlab 2013b (The MathWorks, Inc., Natick, USA) in combination with a Teensy 3.1 microcontroller. To reliably record

MEPs in both muscles, the stimulation intensity used was 130%rMT as described previously (Alaerts, de Beukelaar, Swinnen, & Wenderoth, 2012; Alaerts, Heremans, Swinnen, & Wenderoth, 2009).

From the EMG data, peak-to-peak amplitudes of the MEPs were calculated using custom-made Matlab scripts (Matlab 2015, Mathworks, Natick, MA, USA). Data preprocessing was done using the same criteria presented previously (Cretu et al., 2019). Shortly, the root mean square (rms) of background EMG in the period 110 to 10ms before the TMS pulses was calculated and MEPs with background rms higher than 10 µV were excluded. Additionally, the mean and standard deviation of the background EMG was calculated for each subject and over all trials and MEPs with background rms exceeded 2.5 standard deviations above the mean were removed. Finally, MEPs with a peak-to-peak amplitude smaller than 50 µV were also eliminated from further analyses. Following these criteria, a total of 3.88% of all trials were removed from the data. For the remaining MEPs, the mean peak–to-peak amplitude was calculated separately for each muscle, grasp type, target and task condition.

2.3.4. TMS analysis

Both action execution and action observation studies found that the FDI versus ADM muscle are preferentially activated in PG and WHG, respectively (e.g.: Cavallo, Bucchioni, Castiello, & Becchio, 2013; Lemon, Johansson, & Westling, 1995; Sartori, Bucchioni, & Castiello, 2012), In order to quantify such grasp specific changes in M1 we determined an index of MEP modulation. For each muscle (i.e., FDI and ADM) we calculated whether observing a whole-hand grip versus a precision-grip modulated the MEP amplitude:

$$MEP_{mod} = \frac{MEP_{WHG} - MEP_{PG}}{mean(MEP_{WHG}, MEP_{PG})}$$

Action-specific motor resonance is signaled by positive MEP_{mod} values for the ADM, indicating a stronger facilitation during WHG than PG observation, and negative MEP_{mod} values for the FDI muscle, indicating a stronger facilitation during PG than WHG observation.

2.3.5. Statistical analysis

MEP_{mod} was calculated for each subject, muscle and condition and subjected to RM-ANOVA as dependent variable. We employed muscle (FDI, ADM), target (target, non-target) and task (reward, count) as within-subject factors. As a follow-up analysis, we performed one sample t-tests to determine whether MEP_{mod} is larger than 0 for ADM and smaller than 0 for FDI as predicted for an action-specific modulation. Since we had a strong a-priori hypothesis, these tests were one-sided.

3. Results

3.1. Experiment 1: High rewards lead to decreased response time variability

The results of the behavioral paradigm showed no significant difference in mean response time between the high reward, low reward and counting conditions (p = 0.436; Table 1). Participants needed approximately 350 ms to respond to target actions, independent of task instructions. Additionally, no difference was found in the gaussian mean mu (p = .735).

When comparing the effects of high reward, low reward and counting on the ex-Gaussian model parameters, we found a significant difference in sigma (p = 0.018; $\eta^2 = 0.094$, Table 1 and **Figure 4**), representing the standard deviation of the Gaussian component and is related to intra-subject RT variability. Post-hoc analyses revealed that the average sigma in the high reward condition was significantly smaller than the counting ($p_{FDR} = 0.011$, Cohen's d = 0.576) as well as the low reward condition ($p_{FDR} = 0.013$, Cohen's d = 0.542). No difference was found between sigma in the low reward and count condition ($p_{FDR} = 0.992$). No reward versus counting differences were found for the exponential distribution tau (p =.710). These results suggest that task instructions affect the variability of the responses (i.e., sigma) but not the processing, motor or decisional speed (represented by mean, mu and tau) of the participants. This indicates that actions associated with a high reward were more precise (i.e., less variable) compared to low or no monetary reward.

Table 1 Descriptive and RM ANOVA results for the RT distribution parameters.

	Descriptive statistics			RM ANOVA		
	Mean ± SD (ms)			F values	P values	Partial η^2
	Low	High	Count			
mean RT	354.5 ± 33.02	352.2 ± 31.48	353.9 ± 29.79	0.839	0.436	0.020
mu	310.9 ± 33.31	309.4 ± 33.40	311.8 ± 31.54	0.319	0.735	0.007
sigma	**25.08 ± 9.05**	**20.57 ± 7.52**	**24.89 ± 7.49**	**4.230**	**0.018**	**0.094**
tau	44.13 ± 16.55	42.41 ± 17.75	42.10 ± 18.17	0.344	0.710	0.008

RM, repeated measures; Degrees of freedom = 41. Significant p-values are represented in bold (p<0.05).

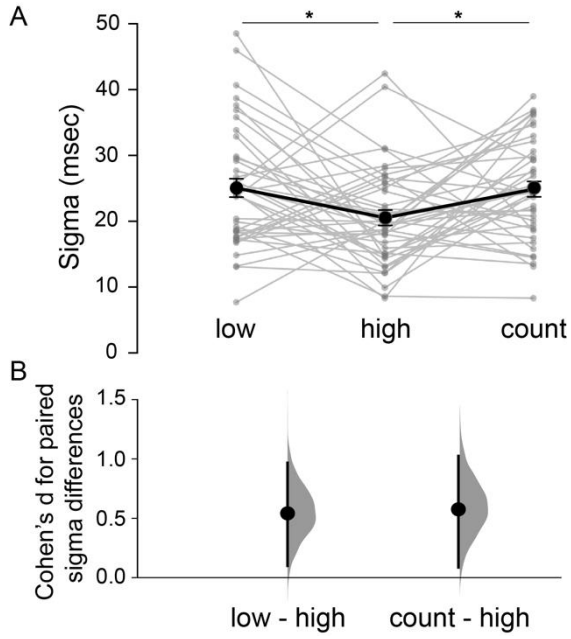

Figure 4 Behavioral results (N = 42)

A) Raw sigma values in function of task instructions (i.e., low reward, high reward, counting; n = 42). B) Effect sizes (Cohen's d) for significant paired sigma differences are depicted as dots. Filled curves depict the resampled distribution of the sigma differences, given the observed data, and error bars depict 95% confidence intervals. *P < 0.05 [false discovery rate (FDR)-corrected t-tests].

Furthermore, the number of errors executed within low, high or count blocks were not significantly different (all p >= 0.37) showing that behavioral performance was unaffected by the task instructions. Thus, we can safely assume the load on working memory resources were similar across the different conditions. Results of the descriptive statistics, as well as the repeated measures ANOVA performed on the error rates are presented in Table 2.

Table 2 Results of descriptive and RM ANOVA analysis performed with error rates.

	Descriptive statistics			RM ANOVA		
	Mean ± SD (ms)			F values	P values	Partial η^2
	Low	High	Count			
errors counting blocks	0.40 ± 0.79	0.29 ± 0.65	0.36 ± 0.48	0.482	0.592	0.010
early presses	0	0.021 ± 0.14	0	1	0.372	0.021
late presses	0.62 ± 1.15	0.59 ± 1.13	0.78 ± 1.14	0.481	0.620	0.010
wrong presses	0.62 ± 0.87	0.51 ± 1.08	0.47 ± 1.02	0.310	0.734	0.007

RM, repeated measures; Degrees of freedom = 46. Significant p-values are represented in bold (p<0.05).

3.2. Experiment 2: Reward driven sharpening of muscle-specific M1 excitability

We probed the action-specific changes in M1 corticomotor excitability in FDI and ADM muscles during the observation of target (i.e., task-relevant) or non-target (i.e.., task irrelevant) grasping actions embedded in a rewarding (i.e., reward task) or an attentional context (i.e., counting task).

Our results indicate that observing a whole-hand grip versus a precision-grip lead to differential modulation of MEP amplitude in the two muscles (i.e., on average we found $MEP_{mod} < 0$ for FDI and $MEP_{mod} > 0$ for ADM; main effect of muscle $p<.001$, $\eta^2 = 0.423$). Furthermore, this action-specific corticomotor excitability was stronger when observed grasping actions were rewarded versus counted (muscle x task $p = .047$, $\eta^2 = 0.114$), as well as when observed grasps was the target action (muscle x target $p = .014$, $\eta^2 = 0.17$), as can be seen in **Figure 5** and Table 3.

To better understand the effects of action-value on motor resonance, we calculated a reduced statistical model, separately for the target and non-target actions. Results showed that during the observation of target grasps, action-specific modulation of MEPs is present and influenced by the reward versus counting instructions (muscle $p < 0.001$, $\eta^2 = 0.452$; muscle x task $p = .025$, $\eta^2 = 0.144$). Monetary rewards caused a significantly stronger change in action-specific MEP modulation (Cohen's d = 1.08) than simple attention, as tested in the counting task (Cohen's d = 0.54). When the non-targeted grasp is observed, action-specific modulation is strongly suppressed (muscle p = .26) and no difference exists between the reward and the counting condition (task p = .37).

Table 3 RM ANOVA results for TMS experiment (N = 34)

	F values	P values	Partial η^2
Main Effects			
Muscle (FDI, ADM)	**24.158**	**<0.001**	**0.423**
Task (reward, count)	0.165	0.688	0.005
Target (target, non-target)	3.59	0.067	0.098
Interactions			
Muscle x Task	**4.244**	**0.047**	**0.114**

Muscle x Target	**6.753**	**0.014**	**0.17**
Task x Target	0.838	0.367	0.025
Muscle x Task x Target	1.722	0.199	0.05
Target action			
Muscle (FDI, ADM)	**27.27**	**<0.001**	**0.452**
Task (reward, count)	0.539	0.468	0.016
Muscle x Task	**5.55**	**0.025**	**0.144**
Non-target action			
Muscle (FDI, ADM)	1.293	0.264	0.038
Task (reward, count)	0.823	0.371	0.024
Muscle x Task	0.053	0.820	0.002

ADM, abductor digiti minimi; FDI, first dorsal interosseous; RM, repeated measures; Degrees of freedom = 33. Significant p-values are represented in bold ($p<0.05$).

Follow-up analyses testing whether MEP_{mod} deviated significantly from zero revealed action-specific facilitation during the observation of rewarded target grasps in both FDI (p_{FDR} = .028, Cohen's d = -0.341) and ADM (p_{FDR} <.001, Cohen's d = 0.717) muscles. During the observation of counted target grasps only the ADM muscle showed action-specific facilitation (p_{FDR} <.001, Cohen's d = 0.628).

In summary, this pattern of MEP modulation indicates that action observation activates motor representations specific to different grip types in M1 and that this action specific neural tuning is "sharpened" when a high reward value is associated with the observed movement. This effect appears to be significantly larger than attention per se, as tested in the counting control condition.

Figure 5 Results of TMS experiment (n = 34).

A) Motor- evoked potential (MEP) modulation during the observation of videos depicting a whole hand grip (WHG) or a precision grip (PG) either in a reward (red lines) or counting (blue lines) task. Results are presented separately for each target type and muscle [first dorsal interosseous (FDI) and abductor digiti minimi (ADM)]. Values >0 indicate higher facilitation during WHG vs. PG observation, whereas values <0 indicate increased facilitation during PG vs. WHG observation. B) The action-specificity effect (i.e., ADM – FDI) in each condition is plotted as a bootstrap sampling distribution with Cohen's d effect sizes depicted by the black dots and the 95% confidence intervals indicated by the vertical error bars. *P < 0.05 [false discovery rate (FDR)-corrected 1-sided t-tests].

4. Discussion

In this study, we provide converging evidence in support of the integration of action value into behavioral and physiological outcomes during action observation. In each block, monetary value (i.e., reward condition) or attentional demands (i.e., counting control condition) were associated with one of two observed grasping actions. We show for the first time that highly valued observed actions lead to increased precision (decreased variability) of response times. Additionally, we show that action-specific physiological responses elicited during action observation in humans (i.e., motor resonance) are modulated by the value of observed actions. In particular, our results suggest that a high subjective value in form of monetary rewards sharpens the neural tuning of action representations activated by movement observation. This neural tuning was weaker in the control (counting) task which was

matched in attentional demands, but not associated with any rewards. Therefore, the strengthening of action-specific M1 response is not simply due to differences in the allocation of attention but rather to a more targeted effect of reward on motor resonance.

Our findings regarding the modulation of motor resonance by action value (i.e., in the reward versus counting target conditions) are in good agreement with recent results from single neuron recordings in area F5 of primate premotor cortex (Caggiano et al., 2012). Caggiano and colleagues suggested that mirror neurons are modulated by the subjective value of observed actions, with the majority discharging more strongly during the observation of highly valued actions. Here, we investigated the modulation of action-specific motor resonance elicited in the human M1 during the observation of rewarding actions. Despite the obvious methodological differences between the studies, we complement the single cell results in monkeys by showing a similar strengthening of M1 mirroring during the observation of highly-valued actions. The general assumption is that M1 motor resonance represents a measure of mirror neuron activity. Similar to F5 mirror neurons, corticospinal excitability in M1 is increased during action execution as well as action observation. Importantly, in our study, we computed an action-specific index of mirroring (i.e., MEPmod) which can be used to characterize the specificity of M1 modulation during action observation. It is also worth mentioning that in the experiment by Caggiano and colleagues, action value was indicated by the object on which the action was performed (i.e., rewarded versus non-rewarded items). In other words, the same movement type (e.g., PG or WHG, depending on the experiment) was used to grasp objects without any value or, valuable food items which were directly offered to the monkey on a subset of trials. By contrast, in our experiments, the value was directly associated with a specific grasp type at the start of each block, while the grasped item was identical. Nevertheless, similar to their design, we compared signals elicited during the observation of actions associated with reward or not, while levels of attention were similar across conditions. Therefore, our results extend these non-human primate findings by showing that M1 motor resonance integrates information about observed action value.

4.1. Reward influences behavioural responses to action observation

In our experiment, we recorded responses during high reward, low reward and control action observation conditions and found that reward value exerted an effect on the variability of the responses as measured by sigma (representing RT variability.) More specifically, we observed a narrowing of the RT distribution during high reward compared to both low reward and counting conditions. Importantly, this was not due to differences in average response speed or difficulty between the task conditions since we found no mean reaction time difference and no counting performance difference. Our task framing explicitly favoured accuracy over speed while also ensuring that alertness was similar across conditions. Participants' task was to press a button when they saw the target grasp and additionally count either the accumulated reward or the number of observed target grasps.

RT variability reflects an important aspect of executive control and was found to be negatively correlated with motivation levels (Wang, Ding, & Kluger, 2014). Therefore, we can speculate that higher motivation levels in the high reward condition contributed to a narrowing of the RT distribution. Recent studies focusing on eye movements reported a similar improvement in motor precision with increasing reward value (Manohar et al., 2015; Manohar, Muhammed, Fallon, & Husain, 2019).

4.2. Action-specific representation of target versus non-target grasps in M1

We additionally probed the action-specific changes in primary motor cortex during the observation of rewarded or counted grasping movements. Our method offers the advantage of extracting specific information regarding the neural tuning of action representations evoked by movement observation. This is essential when describing the functional role of action value during motor resonance (Alaerts, Senot, et al., 2010; Alaerts, Swinnen, & Wenderoth, 2010; Bunday et al., 2016; Cretu et al., 2019; de Beukelaar et al., 2016). We operationalized action-specific motor resonance as changes in corticomotor excitability as measured with single-pulse TMS simultaneously in the first dorsal interosseous (FDI) and the abductor digiti minimi (ADM) muscles when subjects observed whole-hand versus precision grip actions.

M1 was modulated in an action-specific manner during the observation of the targeted grasps when averaged across reward and counting conditions. This finding is in line with previous studies using the same PG versus WHG paradigm. When the observed grasp was the non-targeted action (i.e., non-target: action is not rewarded and not counted), action-specific modulation was strongly suppressed. A similar improvement in neural processing of task-relevant items was found in previous studies and was attributed to differences in selective attention (Banich et al., 2001; Egner & Hirsch, 2005; Gál et al., 2009; Polk, Drake, Jonides, Smith, & Smith, 2008). Importantly, in our experiment, this suppression does not involve a general decrease in corticomotor excitability during non-target grasps. When collapsing across grasp types (i.e., PG and WHG), no differences were observed in the amplitudes of MEPs recorded during target and non-target trials in the two muscles (target effect p=0.194), as shown in **Fehler! Verweisquelle konnte nicht gefunden werden.**.

4.3. Reward sharpens the neural tuning of action representations in M1 during action observation

We are the first to show that monetary rewards associated with observed actions strengthen action-specific motor resonance (Cohen's d = 1.09) beyond the modulation already induced by task-relevant attention-driven salience (Cohen's d = 0.54). Note that reward and counting conditions were closely matched, since participants had to count either the accumulated rewards or the occurrence of the target

grasp while the overall protocol as well as the action stimuli were identical. Although it is difficult to strictly dissociate attention and reward-related effects, we argue that the strengthening of action-specific signals during movement observation can be uniquely attributed to the latter. In essence, our results suggest that reward modulates action-specific motor resonance through the amplification of task-relevant information (**Figure 5**).

This is consistent with recent insights into the mechanisms of reward-based modulation which support an improvement of the signal-to-noise ratio of task-relevant characteristics (e.g., Engelmann and Pessoa, 2007; Etzel et al., 2008; Baldassi and Simoncini, 2011; Chelazzi et al., 2013; Grueschow et al., 2015; Zhang et al., 2018). Etzel and colleagues (2016) used pattern classification methods and showed that task rules were decoded more effectively on reward trials. In agreement to our findings, they proved that reward does not only lead to a generalized increase in brain activity but rather an enhancement of task-relevant representations.

Similarly, attention to task-relevant features can also lead to a selective increase in the responses of neurons that respond to those features (Maunsell & Cook, 2002). One idea is that when a feature is expected because of task instructions, neurons encoding that feature will respond more strongly. This is in line with the *sharpening* hypothesis in which bottom-up sensory signals that are congruent with prior expectations are relatively enhanced (Lee & Mumford, 2003). Therefore, we might argue that attention and reward both lead to a sharpening of task-relevant features but that overall increased attention is directed towards those stimuli which are associated with rewards (Maunsell, 2004). Chelazzi and colleagues, (2013) proposed a very interesting mechanism through which this might happen. They indicated that when rewards are used as incentives for motivation (which we can assume to be the case in our study), this leads to increased top-down attention towards target stimuli. Attention will then impact perceptual processing which in turn will enhance the representation of rewarded target stimuli in a bottom-up manner. Therefore, an interplay between top-down motivation and bottom-up increased salience could explain the strengthening of the action-specific MEP modulation during the observation of rewarding actions in our experiment. This is in line with recent findings suggesting that when value is associated with specific stimuli, these will subsequently have increased attentional priority (Anderson, 2013; Hickey, Chelazzi, & Theeuwes, 2010).

One interesting new aspect provided by our study is that in the context of movement observation, reward-induced sharpening of neural information can be demonstrated for primary motor cortex, suggesting that reward effects are not limited to perceptual processing. Considering that Caggiano et al., (2012) found a similar modulation in PMv mirror neurons, this region might have exerted a modulatory effect on M1. In fact, PMv - M1 action-specific interactions have been demonstrated previously, thus it is reasonable to suggest that the strengthening of action-specific information M1 is mediated by PMv (Davare, Lemon, & Olivier, 2008; Davare, Montague, Olivier, Rothwell, & Lemon,

2009; de Beukelaar et al., 2016; Fluet, Baumann, & Scherberger, 2010). If PMv neurons fire more for observed actions associated with high subjective value, then M1 activity might become proportionally stronger during the observation of these actions. Therefore, highly-valued actions could lead to the optimization of PMv-M1 interactions, potentially signalling increased importance and relevance of the respective rewarding movements compared to non-rewarding ones.

4.4. Potential neural mechanisms responsible for the observed effects

Although our study cannot unveil the neural substrates responsible for the observed effects, transcranial magnetic stimulation reveals the net effects of reward on muscle-specific corticomotor excitability in M1.

Several studies observed that M1 excitability is modulated by direct rewards or by reward expectation during motor tasks (Bundt, Abrahamse, Braem, Brass, & Notebaert, 2016; Gupta & Aron, 2011; Kapogiannis et al., 2008; Klein-Flugge & Bestmann, 2012; Mooshagian, Keisler, Zimmermann, Schweickert, & Wassermann, 2015; Suzuki, Hamaguchi, & Matsunaga, 2018; Suzuki et al., 2014; Thabit et al., 2011). It is also clear from the literature that many brain areas involved in reward processing, such as striatum, ventral tegmental area (VTA), anterior cingulate cortex (ACC), supplementary motor area (SMA), orbitofrontal cortex and amygdala, are influencing premotor and motor cortices (Campos, 2005; FitzGerald, Friston, & Dolan, 2012; Gottfried, O'Doherty, & Dolan, 2003; Hosp, Pekanovic, Rioult-Pedotti, & Luft, 2011; Kunori, Kajiwara, & Ichiro Takashima, 2014; Leemburg, Canonica, & Luft, 2018; Schultz, 2000; Wickens, Reynolds, & Hyland, 2003; Williams, Bush, Rauch, Cosgrove, & Eskandar, 2004).

Because M1 receives direct and indirect inputs from many structures involved in reward processing, we can speculate that dopaminergic projections shape neural action representations associated with rewarded target grasps. Indeed, it has been shown that reward value can shape the tuning curves of motor-related neurons via the dorsal striatum in monkeys (Pasquereau et al., 2007). Due to the slower rise of reward signals in motor cortex, recent findings suggested that reward might influence M1 via indirect basal ganglia-thalamo-cortical loops (Ramkumar, Dekleva, Cooler, Miller, & Kording, 2016).

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