Timing of mirror system activation when inferring the intentions of others

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## Abstract

Neuroimaging studies have shown mirror system (MS) activation when participants infer internal states e.g. emotions, intentions or beliefs (known as ‘mentalizing’) from others’ actions. However, the exact role of the MS in mentalizing tasks is unknown. Dysfunctional MS activation may underlie mentalizing deficits experienced by adults with autism spectrum disorder (ASD). This study investigated the timing of MS activity when inferring intentions in order to delineate between existing models of MS involvement. Single-pulse transcranial magnetic stimulation (TMS) was applied to the primary motor cortex at different time points during the observation of hand actions whilst participants inferred intentions (mentalizing task) and performed a non-mentalizing task. Electromyographic activity in the contralateral hand was used as an indirect measure of MS activity. Greater corticospinal activity was found during the mentalizing task than the non-mentalizing task, but only at the end of observed actions, suggesting late MS involvement in processing intentions. Enhanced corticospinal activity was not related to autistic traits or behavioural performance suggesting the MS has a more automatic role in processing others’ intentions, irrespective of mentalizing ability. Our results extend current knowledge of MS activation when mentalizing, allowing initial delineation between different models of MS involvement in mentalizing.

Keywords: Mirror neuron system, mentalizing, intentions, transcranial magnetic stimulation (TMS), autistic traits

## Introduction

The mirror system (MS) is a network of brain areas, discovered in monkeys, that contain neurons that are active both when an individual performs an action and when they observe others performing similar actions (di Pellegrino, Fadiga, Fogassi, Gallese, & Rizzolatti, 1992; Rizzolatti, Fadiga, Gallese, & Fogassi, 1996). A similar system is thought to exist in the human, and the main components are considered to be the inferior frontal gyrus (IFG) and the inferior parietal lobe (IPL; Rizzolatti & Craighero, 2004; Rizzolatti & Sinigaglia, 2010). It is thought that the human MS plays an important role in interpreting others’ actions (Gallese & Goldman, 1998; Rizzolatti & Craighero, 2004). In addition, when action kinematic information is available, it has been proposed that the MS is required in order to infer others’ internal states (e.g. emotions, beliefs or intentions; collectively referred to as ‘mentalizing’). Indeed, mentalizing tasks that have used stimuli which either include movies of human actions or portray human actions (through sets of still images or point-light displays), have tended to elicit MS activity (Brunet, Sarfati, Hardy-Baylé, & Decety, 2000; Bucchioni, Cavallo, Ippolito, Marton, & Castiello, 2013; Centelles, Assaiante, Nazarian, Anton, & Schmitz, 2011; Ciaramidaro, Becchio, Colle, Bara, & Walter, 2014; Enticott et al., 2013; Iacoboni et al., 2004). Although there is evidence that the MS is active when inferring others’ internal states from their actions, the exact role of the MS in this task is debated.

There are a number of different theories regarding the involvement of the MS in inferring other’s internal states from their actions: 1. The motor simulation theory states that MS activity alone, reflecting simulation of observed actions by the observer’s own motor system, is sufficient to derive others’ internal states (Rizzolatti & Sinigaglia, 2007); 2. A dual-process hypothesis has been proposed which suggests that internal state information embedded in action kinematics is subconsciously processed in the MS and this information is then passed on to a separate cortical system known as the ‘mentalizing system’ in order for make active inferences about the person’s internal state (de Lange, Spronk, Willems, Toni, & Bekkering, 2008; Keysers & Gazzola, 2007; Spunt & Lieberman, 2012c; Uddin, Iacoboni, Lange, & Keenan, 2007); 3. The ‘mirroring-first’ model implies that processing action kinematics in the MS is a vital prerequisite for inferring others’ internal states but the MS is not involved in processing others’ internal states itself (Hamilton & Marsh, 2013; Spunt, Satpute, & Lieberman, 2011).

A strict ‘mirroring-first’ model cannot account for the evidence which shows that MS activity is modulated by mentalizing (Brunet et al., 2000; Bucchioni et al., 2013; Centelles et al., 2011; Ciaramidaro et al., 2014; Enticott et al., 2013; Iacoboni et al., 2004). However, one possible source of this MS modulation could be feedback from the mentalizing system. The predictive coding theory suggests that when inferring aspects of someone’s internal state from their actions, contextual information is processed prior to kinematic processing (Csibra & Gergely, 2007; Kilner, Friston, & Frith, 2007). This contextual information is used to infer the internal state of the individual and therefore predict the outcome of upcoming actions. These predictions are then signalled to the MS and incoming sensory information is compared to predictions made. Discrepancies between predictions made and actual action outcomes are signalled in the form of ‘prediction errors’ and these are used to update future predictions (Kilner, Neal, Weiskopf, Friston, & Frith, 2009). Alexander and Brown’s predicted response outcome model (Alexander & Brown, 2011) suggests that the medial pre-frontal cortex (mPFC), a core area of the mentalizing system, makes predictions about the outcomes of upcoming actions based on action context and prior experience. Therefore, the predictive coding model, in combination with the predicted response outcome model, suggests a potential fourth model of MS involvement: information regarding others’ internal states is processed by the mentalizing system (mPFC) first based on contextual information before internal states are processed in the MS. Data from neuroimaging studies have provided evidence to support this model: action context and prior expectations about an upcoming action modulate activity in the mPFC (Alexander & Brown, 2011; Becchio et al., 2012; Chambon et al., 2017b; Cooper, Kreps, Wiebe, Pirkl, & Knutson, 2010; Ferdinand & Opitz, 2014; Fogelson, Shah, Scabini, & Knight, 2009; Forster & Brown, 2011; Jahn, Nee, Alexander, & Brown, 2014; Leue, Cano Rodilla, & Beauducel, 2015; Schiffer, Krause, & Schubotz, 2014) and increased functional connectivity between the mPFC and the MS has been reported when inferring internal mental states from actions (Ciaramidaro et al., 2014; Spunt & Lieberman, 2012a; 2012b). Additionally, action context has been shown to modulate MS activity (Amoruso, Finisguerra, & Urgesi, 2016; Amoruso & Urgesi, 2016; Iacoboni, Molnar-Szakacs, Gallese, Buccino, & Mazziotta, 2005), possibly via top-down connectivity from the mentalizing system to the MS.

Understanding *when* MS activity is modulated by mentalizing may help delineate the possible roles of the MS in the mentalizing process. Previous studies have shown that the early kinematics of actions vary depending on the actor’s underlying intentions and intentions can be predicted from this information before the outcomes of the actions have been revealed (Manera, Becchio, Cavallo, Sartori, & Castiello, 2011; Sartori, Becchio, & Castiello, 2011). Both the motor simulation theory and dual-process hypothesis suggest that when inferring intentions from actions, MS activity should be observed early during action observation whilst kinematic differences reflecting the actor’s intention are available and processed. In contrast, the predictive coding framework suggests that predicted intentions of others are first processed in the mentalizing system and, therefore, mentalizing-induced modulation of MS activity would be observed later following top-down signalling of action predictions. Finally, the strict ‘mirroring-first’ model would suggest that MS activity shows little modulation by the process of mentalizing.

Previous studies have used transcranial magnetic stimulation (TMS) to investigate the timing of MS modulation due to the high temporal resolution of this technique (Amoruso, Finisguerra, & Urgesi, 2016b; Barchiesi & Cattaneo, 2013; Bardi, Schiff, Basso, & Mapelli, 2015; Candidi, Sacheli, Mega, & Aglioti, 2014). Single TMS pulses can be applied at different time points during action observation in order to provide an indirect measure of MS activity at different stages of an action. For example, Alaerts and colleagues found that the weight of objects being acted upon influenced MS activity during early stages of action observation even before the objects had been grasped (Alaerts, de Beukelaar, Swinnen, & Wenderoth, 2012). These results suggest that the MS represents predictions about upcoming actions based on properties of the objects being acted upon as well as the kinematics of the goal directed action. In contrast, Amoruso and colleagues found that when participants were inferring the goals of observed actions, action context only modulated MS activity during later stages of the actions (Amoruso et al., 2016). This shows that the MS is not involved in early processing of action context when making predictions about the goals of observed actions. Collectively, these data suggest that different factors modulate MS activity at different time points during action observation. In the current study, we used single-pulse TMS in order to determine when mentalizing modulates MS activity in order to help delineate the role of the MS when inferring the intentions of others’ from their actions.

Determining the role of the MS in inferring others’ intentions from actions is of potential importance in understanding autism spectrum disorder (ASD) which is associated with difficulties inferring the intentions of others (Happé, 1994; Kana, Libero, Hu, Deshpande, & Colburn, 2014; Moran et al., 2011). The ‘broken mirror’ theory proposes that these individuals exhibit atypical MS activity (Iacoboni & Dapretto, 2006; Oberman & Ramachandran, 2007; Ramachandran & Oberman, 2006), and this underlies difficulties these individuals experience in inferring the internal states of others, and consequently contribute to the social interaction deficits associated with ASD (American Psychiatric Association, 2013). ASD is a spectrum disorder, meaning that individuals within the non-clinical population exhibit differing degrees of autistic traits (Robinson et al., 2011). Individuals with relatively high levels of autistic traits without a diagnosis, have been shown to display reduced abilities to infer the internal states of others (Baron-Cohen, Wheelwright, Hill, Raste, & Plumb, 2001; Gökçen, Petrides, Hudry, Frederickson, & Smillie, 2014; Gökçen, Frederickson, & Petrides, 2016) and atypical MS activity (Cooper, Simpson, Till, Simmons, & Puzzo, 2013; Lepage, Tremblay, & Théoret, 2010; Puzzo, Cooper, Vetter, Russo, & Fitzgerald, 2009). Collectively, these data suggest that the level of autistic traits displayed may correlate with MS functioning and abilities to infer intentions. In this study we, therefore, evaluated the degree of autistic traits displayed by participants in order to examine whether this factor influenced the level of MS activity displayed when inferring others’ intentions.

The present study aimed to investigate MS activity at different time points during three different tasks in order to delineate between previously proposed models of the role of the MS in inferring intentions from actions. Single-pulse TMS was applied at different time points during action observation whilst participants inferred the actors’ intentions (Mentalizing task), whilst participants observed actions that did not depict the actors’ intentions and participants were not required to mentalize (Action task), and whilst participants observed actions that reflected the actors’ intentions but participants were not required to mentalize (Either task). If the motor simulation theory explains the role of the MS in mentalizing, early MS modulation would be observed during the Mentalizing task, and MS activity during this task should correlate with ability to infer intentions. If the dual-process hypothesis explains the role of the MS in mentalizing, early MS modulation would be observed during both the Mentalizing and the Either task, but MS activation should not correlate with behavioural performance. If intentional information is processed by an alternative cortical system first (e.g. the mentalizing system) then MS modulation would be expected only at later stages of the observed actions during the mentalizing task. Finally, the mirroring-first model would predict equivalent levels of MS activity across all tasks throughout action observation as the MS should not specifically be involved in deriving intentions. Autism quotient (AQ) scores were also measured for all participants in order to perform an exploratory analysis examining whether the level of autistic traits participants displayed correlated with the degree of mentalizing-induced MS modulation. Individuals with higher levels of autistic traits were expected to exhibit lower levels of MS modulation (cf. Dapretto et al. 2006).

## Method

### Participants

Participants were recruited based on their Autism Quotient (AQ) scores (Baron-Cohen et al., 2001) in order to ensure there was a wide range of AQ scores among participants. An email was sent to students at the University of York containing a link to an online version of the 50-item AQ questionnaire. Six hundred and four students responded and completed the AQ assessment. Fifteen participants were recruited (9 female) aged 18-29 (mean=22.13, SD=3.14) with AQ scores ranging from 4-40 (mean=18, SD=11.99). All participants reported no neurological or psychiatric illnesses, no contradictions for TMS and provided written informed consent. None of the participants had a diagnosis of ASD. Ethical approval was granted by the York Neuroimaging Centre Ethics Committee. All research was performed in accordance with the ethical standards laid down in the 1990 Declaration of Helsinki.

### Stimuli

The stimuli used were a subsample of the movies used in a previous behavioural study (Cole, Slocombe, & Barraclough, 2018), and are described in detail there. Briefly, movies were filmed at full HD (1080 x 1920 pixels) and at 50 frames per second using a Panasonic TM900 camera. Actors were filmed sitting in front of a white wooden board and passing or attempting to pass poker chips to another player (out of view) through slots cut out of the board (see Figure 1). Actors each performed ten different actions; five hand actions involved pushing poker chips with their right index finger towards a slot level with the surface of the table in front of them. The other five hand actions involved grasping the poker chips with their right index finger and thumb and lifting the chips towards a slot at head height. Both pushing and grasping actions were executed by the actor in one of 5 different ways: 1. clumsily failing to pass one poker chip; positive intention to pass the chip, but the outcome of the action was unsuccessful (clumsy 1), 2. Clumsily failing to pass five pokers chips (clumsy 5), 3. Spitefully failing to pass one poker chip; no intention to pass the chip and the outcome of the action was unsuccessful (spiteful 1), 4. Successfully passing one poker chip (successful 1) and 5.Successfully passing five poker chips (successful 5). Two types of actions (grasping and pushing) were used in order to make the stimuli more varied and these particular actions were chosen as they both utilize the first dorsal interosseous (FDI) and opponens pollicis (OP) muscles. Sets of movies of 12 different actors (6 female and 6 male) were used for this experiment.

[FIGURE 1 ABOUT HERE]

### Electromyography and TMS

Electromyogram (EMG) was recorded from the FDI and OP muscles of the left hand using standard surface Ag-AgCl electrodes. Participants’ left arms were rested on the table in front of them. EMG signals were band-pass filtered and amplified using a BIOPAC MP150 amplifier (BIOPAC Systems Inc., USA). The top centre point of the head (Cz) was found by measuring half way between the inion and the nasion as well as the half way point between the ears. The position of the hand area of right primary motor cortex (M1) was identified in participants by measuring 5cm lateral and 1cm anterior to Cz. A 3-by-3 grid was created around the estimated position of right M1. Single TMS pulses were delivered using a Magstim Rapid2 and a 70mm figure of eight coil to every point in this grid (Magstim Company Ltd, UK). The point in the grid that produced the largest motor evoked potentials (MEPs) in the left FDI & OP muscles when stimulated was concluded to be the optimal stimulation site in M1. The resting motor threshold was determined for each participant as the minimum stimulation intensity that produced MEPs greater than 50µV amplitude in the FDI and OP muscles in 5/10 cases after single pulse stimulation. The TMS pulses delivered during the experiment were at 120% resting motor threshold (mean stimulator output=64.7%, SD=8.4).

### Procedure

Before starting the experiment, each participant played a poker chip game with the experimenter. This was done in order to familiarise participants with the board and poker chips they would see in the movies and so they understood the aim of the game was to have the highest number of poker chips on your side of the board as possible. For a full description of this poker chip game, see the previous behavioural experiment (Cole et al., 2018).

During the experiment, MATLAB (MathWorks Inc., Massachusetts, USA) was used to run the experiment, record participants’ responses and send TTL pulses to the parallel port in order to trigger the delivery of TMS pulses. Movies were displayed on a 22” flat-screen CRT monitor (Philips 202P40, 1600 x 1200 pixels 100Hz refresh rate) positioned approximately 60cm in front of participants. Each trial consisted of two action movies of the same type (either grasping or pushing) presented sequentially with an inter-stimulus interval of 1000ms. During the inter-stimulus interval, the screen was black except for a white fixation cross. Following the presentation of the second stimulus a response screen was displayed which read ‘Actor 1 or Actor 2?’ and participants had to indicate whether they would rather play the poker chip game with the actor in the first or second movie by pressing either ‘1’ or ‘2’ on the keyboard with their right hand. Movies were presented in blocks of ‘Mentalizing’, ‘Either’ or ‘Action’ tasks and all movies were shown in greyscale. Despite the instructions being the same for all blocks, the inferences which had to be made in order to select between actors differed across tasks. During the Mentalizing task, actions with different intentions but the same outcome were shown (clumsy 1 and spiteful 1). Here, in order to make the appropriate decision between the actors, participants were required to infer the intentions of the actors. There were two types of control tasks: Either and Action tasks. During the Action task, pairs of successful actions were presented in which one actor passed one poker chip (successful 1) and another actor passed five poker chips (successful 5). In order to make the appropriate decision during this task, participants simply had to identify which action involved the highest number of poker chips. During the Either task participants were shown two actions with positive intentions but involving different numbers of poker chips (clumsy 1 and clumsy 5). Again, in order to make the appropriate decision, participants simply had to identify which action involved the greatest number of poker chips. However, the movies shown during this task did portray positive intentions of the actors so participants may have automatically inferred the intentions of the actors. This task is referred to as the Either task as it may involve mentalizing or simply action processing. The Either task was included in the experiment in order to control for the fact that the Mentalizing task only showed unsuccessful actions and the Action task showed only successful actions. The Either task showed unsuccessful actions but mentalizing was not required in order to complete the task. Participants completed 12 practice trials, 4 of each task type (Mentalizing, Either and Action), before they took part in the main experiment.

Within each block, every trial showed one action performed by a male actor and one action performed by a female actor. The stimuli were counterbalanced so that gender and identity of the actors were not predictors of the action outcome. There were four blocks of each task, each containing 30 trials (60 movies). Each block contained 15 grasping trials and 15 pushing trials which were randomly presented. Every participant completed all 12 blocks across two sessions. In each session participants completed 6 blocks (2 of each task type). The order in which blocks (n=12) were completed was different for every participant. Additionally, the order in which different tasks (Mentalizing, Either, Action) were completed was counterbalanced across participants and the order in which each participant completed the different task types in the first session was reversed in the second session. This was done to reduce the possibility of order effects. Each block lasted approximately 8 minutes and participants had short breaks in between each block. The two TMS sessions were completed on separate days but all elements of the experiment were completed within a 2 week period.

Single TMS pulses were delivered at one of six different time points during each movie. The movies were made in a controlled way so that TMS pulses could be applied during specific stages of every action. In all movies, the poker chips were released 20 frames before the end of the movie, the actors were stationary for at least the first 25 frames of every movie and the frame in which the poker chip was first grasped/pushed was recorded for each movie. Therefore, the pulse timings were defined in the following way: Pulse time 1 was at the start of the movie before movement occurred (frame 20), pulse time 2 was after movement onset but before contact had been made with the poker chip(s) (20 frames before the frame in which the poker chip(s) were first grasped/pushed), pulse time 3 was when the poker chip(s) were first grasped/pushed (between frames 73-161), pulse time 4 was during the action before the poker chip(/s) left the actor’s hand (15 frames after the frame in which poker chip(s) were first grasped/pushed), pulse time 5 was at the moment at which poker chip(/s) left the actor’s hand (frame 180) and pulse timing 6 was at the end of the action after the poker chip(/s) had been released (frame 200; see Figure 2). The action outcome was evident from time point 5 (the point at which the poker chip was released). There were 20 repeats of each of the 36 conditions [pulse time (1-6), task (Mentalizing, Either, Action) and action type (grasping or pushing)]. The time at which TMS pulses were delivered was counterbalanced across task and action types.

[FIGURE 2 ABOUT HERE]

## Analysis

### Behavioural data

The mean proportion of correct responses were calculated for each task for every participant. Data screening identified that these data were not normally distributed and consequently, a log transformation was applied. Following the log transformation, the data still violated the assumption of normality so non-parametric analyses were conducted. A Friedman’s ANOVA was used to examine potential differences in behavioural performance across tasks. The relationships between task performances and both levels of autistic traits and MS activity were investigated using linear regression analyses.

### MEP data

For each participant, the mean and standard deviation of the root mean squared scores of the EMG background activity in the 50ms period prior to stimulus onset were calculated. As EMG background activity can modulate MEP magnitude (Hess, Mills, & Murray, 1987), MEPs were excluded from the analyses if EMG background activity exceeded more than 2.5 standard deviations (SD) from the mean EMG activity for that particular participant and muscle. MEP peak-to-peak amplitudes were measured, and in order to exclude outliers, those MEPs that differed more than 1.5 SD from the mean MEP size for that condition and muscle, were also excluded from subsequent analyses. From the remaining MEPs, median values were then calculated for each muscle and condition. Median MEP values were calculated rather than mean MEP values as Schmidt and colleagues showed that MEP values can be inflated on initial trials (Enticott et al., 2011; Schmidt et al., 2009) and this would have greater influence on mean rather than median values. In total, 12.07% of all MEPs were excluded from the analyses, and the proportion excluded/condition are reported in Table 1 in the supplementary materials.

The median MEP values were averaged across both muscles (FDI and OP) and action type (pushing and grasping) as neither were factors of interest; the goal of the experiment being to investigate the effect of the interaction between TMS pulse timing and task on MEP sizes. This resulted in 18 median MEP values for each participant: for the 6 different TMS pulse timings, and for all three tasks (Mentalizing, Either, Action). Median MEP values violated the assumption of normality and therefore a log transformation was applied. Shapiro-Wilk tests established that median MEP sizes did not significantly differ from a normal distribution after the log transformation was applied. A repeated-measures ANOVA was conducted to identify the influence of task (Mentalizing, Either, Action) and pulse timing (1-6) on MEP sizes. Bayesian ANOVAs and t-tests were conducted to provide evidence for (or against) mentalizing having an influence on mirror system activity at each TMS pulse time point, irrespective of sample size. Bayesian tests are unaffected by the number of participants tested (Dienes, 2011). Finally, linear regression analyses were conducted in order to investigate possible relationships between mentalizing-specific MEP sizes and autistic traits (as measured by AQ). Pearson’s correlation coefficients were calculated alongside all linear regressions and were additionally tested using Bayesian analyses ([Dienes, 2008](#_ENREF_1), [2011](#_ENREF_2)) to quantify the evidence in favor for or against each correlation.

When calculating Bayes factors B quantifies how much more (or less) likely the data are under the alternative hypothesis than under the null hypothesis. For example, B=3.0 would indicate that the data are 3 times as likely to be correlated compared to the null hypothesis, whereas B=1/3 would indicate that the data are 3 times as likely to indicate the hull hypothesis over the alternative that the data are correlated. The suggested convention ([Jeffreys, 1961](#_ENREF_4)) is that Bayes factors above 3 indicate substantial evidence for the alternative hypothesis (data are correlated), Bayes factors below 1/3 indicate substantial evidence for the null hypothesis (data are uncorrelated), whilst values in between 3 and 1/3 indicate neither support for the alternative nor the null hypothesis.

## Results

### Behavioural data

Participants’ abilities to make judgments of the actors’ behaviours were not significantly different across tasks [Mentalizing (proportion correct M=.94, SD=.10), Either (M=.93, SD=.08), Action (M=.93, SD=.06); χ2(2)=5.72, p=.06]. In addition, linear regression analyses showed that the level of autistic traits that participants displayed did not significantly predict performance on the Mentalizing task [F(1,13)=.69, p=.42, R2=.05, r=-.22, B=.69], the Either task [F(1,13)<.01, p=.93, R2=<.01, r=-.03 B=.56] nor the Action task [F(1,13)=1.7, p=.22, R2=.12, r=.34, B=1.02 ]. The Bayes factors indicated that there was evidence neither for, nor against, correlations between the level of autistic traits and performance on any of the tests.

### TMS data

Median MEPs were larger during the Mentalizing task than other tasks when TMS was applied towards the end of the action (see Figure 3A). This was reflected in a significant interaction between task and the timing of the TMS pulse [F(4.71,65.87)=5.11, p=.001, ηp2=.27; Greehouse-Geisser correction applied]. There were no main effects of task [F(2,28)=2.01, p=.16, ηp2=.13] nor TMS pulse timing on MEP sizes [F(2.51,35.20)=1.34, p=.28, ηp2=.09; Greehouse-Geisser correction applied].

The significant interaction between experimental task and TMS pulse timing was explored further by performing six separate Bayesian ANOVAs using Bayesian Information Criteria (JASP Team, 2018; Wagenmakers, 2007), examining the effect of task on MEP sizes at each TMS pulse time separately. At time point 1, the estimated BF10=.56 indicated that that the data is .56 times more likely to occur under a model where participant task had an influence on MEP magnitude, rather than a model without an effect of task. At time point 2, the estimated BF10=.22 indicated that that the data is .22 times more likely to occur under a model where participant task had an influence on MEP magnitude, rather than a model without an effect of task. At time point 3, the estimated BF10=.35 indicated that that the data is .35 times more likely to occur under a model where participant task had an influence on MEP magnitude, rather than a model without an effect of task. At time point 4, the estimated BF10=.29 indicated that that the data is .29 times more likely to occur under a model where participant task had an influence on MEP magnitude, rather than a model without an effect of task. At time point 5, the estimated BF10=1.79 indicated that that the data is 1.79 times more likely to occur under a model where participant task had an influence on MEP magnitude, rather than a model without an effect of task. At time point 6, the estimated BF10=32.75 indicated that that the data is 32.75 times more likely to occur under a model where participant task had an influence on MEP magnitude, rather than a model without an effect of task. Together, these ANOVAs indicated that there is strong evidence for an effect of participant task only at time point 6.

In order to test the effect of mentalizing (Mentalizing task), or potential automatic mentalizing (Either task), compared to the Action task at every TMS time pulse, we calculated a series of Bayesian t-tests. Bayesian t-tests were used to provide evidence for (or against) mentalizing having an influence on mirror system activity at each time point; in addition multiple values needed to be calculated and Bayesian t-tests do not need correcting for multiple comparisons, and are unaffected by the number of participants tested (Dienes, 2011). We found evidence for the effect of mentalizing on mirror system activity at time point 6 (see Figure 3B and supplementary materials Table 2). There was evidence against an effect of both the Mentalizing and Either tasks at all other time points, except the Mentalizing task at time point 5, and the Either task at time point 6, where there was neither evidence for nor against the effect of the tasks.

[FIGURE 3 ABOUT HERE]

Finally, we examined the relationship between mentalizing-specific increases in MEP sizes at time-point 6 and the degree of autistic traits participants displayed. Linear regression analysis showed that participants’ AQ scores did not significantly predict MEP sizes during the Mentalizing task at time point 6 [F(1,13)=.13, p=.72, R2=.01, r=-.10, B=.34]. In addition, the degree of mentalizing-specific MS activity didn’t predict mentalizing behavioural performance [F(1,13)=.93, p=.35, R2=.07, r=-.26, B=.38]. Bayes factors indicated that there was evidence neither for, nor against, correlations between the level of autistic traits and MEP sizes, and between the degree of mentalizing-specific MS activity and performance on the mentalizing task.

## Discussion

This study measured corticospinal activity (as an indirect measure of mirror system (MS) activity) at different time points when inferring the intentions of others, and investigated the relationship between the degree of mentalizing-induced modulation of corticospinal activity and autistic traits. Our results show, enhanced corticospinal excitability when participants inferred actors’ intentions compared to when they made judgments about actions that did not depict the actor’s intention, but importantly only at the end of the actions, when the actors’ intentions had been revealed. No relationships were found between the degree to which corticospinal excitability was modulated and either the level of autistic traits that participants displayed or their behavioural performance. These data help inform models of MS involvement in mentalizing.

The larger MEP sizes (reflecting higher levels of MS activity) found during the Mentalizing task compared to the Action task at the end of observed actions, suggest that the MS plays a role in processing intentional information from hand actions (cf. Buccino et al., 2007; Ciaramidaro et al., 2014; de Lange et al., 2008; Iacoboni et al., 2005; Vingerhoets et al., 2010). These data oppose the mirroring-first hypothesis which argues that processing action kinematics in the MS is a prerequisite for inferring others’ intentions but the MS does not process information about others’ intentions directly (Hamilton & Marsh, 2013; Spunt, Satpute, & Lieberman, 2011). The mirroring-first model predicts that MS activation at all time points would be equivalent irrespective of the task, and this was not observed here.

In contrast, the motor simulation theory argues that MS activity alone is sufficient to infer the intentions of others’ from their actions (Rizzolatti & Sinigaglia, 2007). This theory would predict early mentalizing induced enhancement of MS activity, given previous studies have shown others’ intentions can be inferred during the early phases of their actions (e.g. Manera, Becchio, Cavallo, Sartori, & Castiello, 2011; Sartori, Becchio, & Castiello, 2011). The late timing at which mentalizing was found to modulate MEP sizes provides evidence against this idea and suggests instead that the early information about an individual’s intentions available from actions may be processed in an alternative system prior to MS involvement (Amoruso et al . 2016). In addition, a motor-simulation account would predict that MS activity determines behavioural performance; we did not see evidence for a relationship between the degree of mentalizing-induced modulation of MS activity and ability to infer the intentions of others in our study. Indeed, Bayes factor of .38 indicated that there was more evidence for the null hypothesis: that the mentalizing induced signal we observed in the MS did not determine behavioural performance. Thus, our data are not consistent with the MS directly inferring intentions from observed actions.

The lack of a relationship between mentalizing performance and MS activity potentially supports the dual-process hypothesis which suggests that subconscious processing of intentional information available from action kinematics occurs in the MS first before intentions are actively inferred in the mentalizing system (de Lange et al., 2008; Spunt & Lieberman, 2012b). This theory would not predict a direct relationship between MS activity and mentalizing performance as it argues that the MS is not involved in actively inferring others’ intentions (only passively). However, similar to the motor simulation theory, the dual-process hypothesis would also predict early mentalizing-induced modulation of MS activity, in contrary to our observed results. Instead, the timing of mentalizing-induced modulation of corticospinal activity identified in our study suggests that intentional information is probably processed elsewhere before MS involvement. Predictions about the intentions of unfolding actions, based on prior expectations and action context, may be formed in the mentalizing system prior to intentional inferences made based on kinematic information in the MS (Alexander & Brown, 2011a; Kilner et al., 2007).

The late timing of MS involvement observed in our study suggests that the interaction between the mentalizing system and the MS, when inferring intentions from actions, might be best conceptualized within a predictive coding framework. The predictive coding theory in combination with the predicted outcome response model of mPFC functioning would suggest that intentions are initially inferred based on contextual information in the mPFC before MS involvement in processing intentions information. This is supported by data from neuroimaging studies which have shown that action context and prior expectations about an upcoming action modulate activity in the mPFC (Alexander & Brown, 2011; Becchio et al., 2012; Chambon et al., 2017b; Cooper, Kreps, Wiebe, Pirkl, & Knutson, 2010; Ferdinand & Opitz, 2014; Fogelson, Shah, Scabini, & Knight, 2009; Forster & Brown, 2011; Jahn, Nee, Alexander, & Brown, 2014; Leue, Cano Rodilla, & Beauducel, 2015; Schiffer, Krause, & Schubotz, 2014) and functional connectivity between the mPFC and the MS increases when inferring intentions from actions (Ciaramidaro et al., 2014; Cole, Barraclough & Andrews, 2018; Spunt & Lieberman, 2012a; 2012b). Action context has also been shown to modulate MS activity (Amoruso, Finisguerra, & Urgesi, 2016; Amoruso & Urgesi, 2016; Iacoboni, Molnar-Szakacs, Gallese, Buccino, & Mazziotta, 2005), in the later stages of action processing, possibly via top-down connectivity from the mentalizing system to the MS. If the interaction between the MS and the mentalizing system is conceptualised within a predictive coding framework, the higher activation we found in the MS at the end of observed actions may reflect the signalling of a ‘prediction error’ once the intention of an action has been revealed by the outcome of the action; this prediction error would then be used to update future predictions about others’ intentions (cf. Brown & Brüne, 2012; Kilner, Friston, & Frith, 2007; Kilner & Frith, 2008).

Although mentalizing-specific MS activity and behavioural performance on the Mentalizing task were not correlated in our study, we should be cautious as performances were high (mean proportion of correct responses: M=.94, SD=.10) across participants. Potentially, behavioural performances were near ceiling, obscuring observation of any relationship between mentalizing performance and the degree of mentalizing-specific MS activation to be found. If we had also recruited participants with a diagnosis of ASD, it is possible that these individuals would have displayed poorer performances and a wider range of behavioural performances may have allowed a relationship between mentalizing-induced modulation of MS activity and behavioural performance to be identified. In addition, recruitment of adults with ASD may have allowed a relationship to be identified between autistic traits and mentalizing-induced modulation of corticospinal activity. MS functioning may be atypical in adults with ASD when inferring others’ intentions but reduced levels of MS activity may only be seen in individuals with clinical levels of autistic traits (e.g. see Holt et al., 2014). However, the lack of evidence for a relationship between autistic traits and modulation of corticospinal activity in our study supports some previous studies that found adults with ASD exhibited typical levels of MS activation during mentalizing tasks (e.g. Kana, Keller, Cherkassky, Minshew, & Just, 2009; Kirkovski, Enticott, Hughes, Rossell, & Fitzgerald, 2015). Therefore, it is possible that dysfunction in other brain systems (e.g. the mentalizing system) or dysfunctional connectivity between the MS and the mentalizing system rather than atypical MS activity may underlie the mentalizing deficits that individuals with ASD experience (Frith, 2001; Gallagher et al., 2000; Schurz, Radua, Aichhorn, Richlan, & Perner, 2014; Spunt & Lieberman, 2012b; Spunt et al., 2011).

Other aspects of the different action stimuli may have influenced MS activity in response. First, actions in both the Mentalizing and Either task were always unsuccessful, whilst the actions in the Action task were always successful. Likely reward from actions has been shown to modulate MS activity, where activity is enhanced during the observation of actions with higher likely reward in monkeys (Caggiano et al., 2012; Roesch & Olson, 2003, 2004) and humans (Brown, Wiersema, Pourtois, & Brüne, 2013; Trilla Gros, Panasiti, & Chakrabarti, 2015). For both Mentalizing and Either tasks reward was reduced (no poker chips were passed) and thus we might have expected reduced MS activity if reward was the important factor. Instead we observe enhanced MS activity during the Mentalizing task (but not the Either task). Second, the presence of action errors can also enhance MS activity (Aglioti, Cesari, Romani, & Urgesi, 2008). All actions presented during the Either task showed an actor making an error (they tried to pass the poker chip but clumsily failed); during the Mentalizing task, half the actions involved an error but the other half showed an actor deliberately failing to pass a poker chip, rather than committing an error. If detection of errors was a dominating factor, then we would have observed highest MS activity in the Either task (where both actions contained errors), and a relatively smaller enhancement in MS activity in the Mentalizing task (where only one action contained an error); however, this is the opposite of what we observed here. Third, it is possible that the Either and Action conditions did not require any action processing (only identification of poker chip quantities) and therefore, the higher MS activity found during the Mentalizing task reflects action processing during the Mentalizing task and not the control tasks. However, if action processing occurred during the Mentalizing task and not the control tasks, it would be expected that MS activation would be significantly higher throughout the Mentalizing task. Instead, the significantly higher MS activity only at the end of the observed actions suggests that action processing occurred during all tasks but MS involvement in the later stages of intention processing resulted in significantly higher MEP sizes at the end of observed actions. This argument is supported by previous studies which have shown passively observed actions are processed in the MS (Aziz-Zadeh, Maeda, Zaidel, Mazziotta, & Iacoboni, 2002; Buccino, Binkofski, & Riggio, 2004; Chong, Cunnington, Williams, Kanwisher, & Mattingley, 2008; Luciano Fadiga, Craighero, & Olivier, 2005). Finally, although the hand actions shown in the Mentalizing and Action tasks had very similar kinematics at the time in which the task-related difference in corticospinal excitability was found, they were not identical (see Figure 1). However, in all actions, the poker chip had been released at this time point, and the FDI and OP muscles in the actors’ hands were no longer contracted. Previous studies have shown that increased MEP sizes during action observation are often specific to the muscles involved in the observed actions (Fadiga, Fogassi, Pavesi, & Rizzolatti, 1995; Fadiga, Craighero, & Olivier, 2005; Urgesi, Candidi, Fabbro, Romani, & Aglioti, 2006). Therefore, if MEP sizes were solely dependent upon the simple kinematics of the observed actions, MEPs would be expected to be small in both tasks at this time point (Fadiga et al., 2005; Fadiga et al., 1995; Urgesi et al., 2006); again, this is not what we observed where the MS activity during the Mentalizing task at the end of the action was considerably enhanced. So, although the effects of action error, and the potential likelihood of action reward, and simple action kinematics may have potentially influenced MS activity to some extent, these factors cannot explain the effects we observe here. Instead the dominating influence appears to be the impact of the task that the participants were engaged in.

In the current study, participants observed right-handed actions and MEPs were recorded from the muscles in their left hands. It has been previously shown that MEPs are smaller when they are measured from the hand which is contralateral to the observed hand executing the action compared to when recordings are made from the observer’s hand which is ipsilateral to that of the acting hand (Aziz-Zadeh et al., 2002). In principal, we may have measured larger MEPs if we had applied TMS to the left hemisphere in our study. However, MS activation is bilateral during the observation and imitation of right-handed actions (Caspers, Zilles, Laird, & Eickhoff, 2010). In addition, a previous fMRI study showed bilateral MS activation during the observation of right-handed actions but a greater degree of activation in right MS (Aziz-Zadeh, Iacoboni, Zaidel, Wilson, & Mazziotta, 2004). Higher levels of activity have also been shown in the right MS when actions are shown in a context that reflect the goals of the actions compared to actions shown without context (Kaplan & Iacoboni, 2006). Higher levels of right IFG activity have also been found when inferring the goals of actions compared to processing action kinematics (Spunt & Lieberman, 2011). Finally, reduced activation in right IFG and bilateral IPL in adults with ASD has also previously been associated with poorer abilities to infer the intentions of others (Kana et al., 2014). Collectively, these data suggest that MS activation is often bilateral when observing others’ actions and suggest possible right-hemisphere dominance for MS activity when inferring others’ intentions.

In conclusion our data add to the current knowledge of MS involvement in mentalizing by identifying the timing in which MS activity is modulated by mentalizing. These data allow us to start to delineate between the different models of MS involvement in inferring others’ intentions. The late timing in which MS activity was found to be modulated by mentalizing suggests that the MS plays a role in processing others’ intentions but only once they have been clearly revealed. This points towards the involvement of another cortical system in making early inferences about the intentions of observed actions. MS activity was also found to be independent of behavioural performance and the level of autistic traits displayed by the participants, suggesting that the MS play a more subconscious role in processing the intentions of others’ actions, irrespective of mentalizing ability.

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