Repetitive transcranial magnetic stimulation reveals a role for the left inferior parietal lobule in matching observed kinematics during imitation

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Abstract

Apraxia (a disorder of complex movement) suggests that the left inferior parietal lobule plays a role in kinematic or spatial aspects of imitation, which may be particularly important for meaningless (i.e., unfamiliar intransitive) actions. Mirror neuron theories indicate that the inferior parietal lobule is part of a frontoparietal system that can support imitation by linking observed and stored actions through visuomotor matching, and have less to say about different subregions of the left inferior parietal lobule, or how different types of action (i.e., meaningful or meaningless) are processed for imitation. We used repetitive transcranial magnetic stimulation (rTMS) to bridge this gap and better understand the roles of the left supramarginal gyrus and left angular gyrus in imitation. We also examined if these areas are differentially involved in meaningful and meaningless action imitation. We applied rTMS over the left supramarginal gyrus, left angular gyrus, or during a no-rTMS baseline condition, then asked participants to imitate a confederate's actions whilst the arm and hand movements of both individuals were motion-tracked. rTMS over both the left supramarginal gyrus and the left angular gyrus reduced the velocity of participants' finger movements relative to the actor during imitation of finger gestures, regardless of action meaning. Our results support recent claims in apraxia and confirm a role for the left inferior parietal lobule in kinematic processing during gesture imitation, regardless of action meaning.

Introduction

Neuroscientific research implicates the left parietal lobe in imitation (Caspers *et al.*, 2010; Molenberghs *et al.*, 2009), but neither the precise area nor its exact role are fully established. Some neuropsychologists studying the apraxias - disorders of complex movement in which different types of imitation can be impaired - suggest that the left parietal lobe controls kinematic (Buxbaum *et al.*, 2014) or spatial (Goldenberg, 2009) aspects of imitation, and that the inferior parietal lobule (IPL) in particular is critical for imitating meaningless actions. Theories of social interaction based on the putative human mirror neuron system, by contrast, indicate that the IPL is part of a frontoparietal system that links observed and stored actions through visuomotor matching (Rizzolatti *et al.*, 2014), in terms of movements (Iacoboni, 2009; Iacoboni & Dapretto, 2006) or goals (Hamilton, 2008, 2014). In this way, the IPL could provide a scaffolding for imitation. These theories, however, often say less about the specific role of IPL subregions (supramarginal gyrus, SMG; angular gyrus, AG), or how the left IPL might or might not be differentially involved in meaningful and meaningless action imitation.

These differing views result from different approaches to studying imitation. Neuropsychological studies of apraxia have historically distinguished lesioned regions-of-interest, and compared different types of imitative action (Goldenberg, 2009). However, neuroimaging studies in healthy people have often used only a single or stereotyped action type (e.g., finger tapping) which can make it hard to draw conclusions about different imitative capacities (but see Bien *et al*., 2009; Carmo *et al*., 2012; Decety *et al*., 1997; Grèzes, 1998; Higuchi *et al*., 2012; Koski *et al*., 2003; Krüger *et al*., 2014; Menz *et al*., 2009; Mühlau *et al*., 2005; Rumiati *et al*., 2005; Tanaka *et al*. 2001; Tanaka & Inui *et al*., 2002).

Furthermore, neuroscience-driven work on imitation in healthy individuals is often defined by the experimental scanning environment. Experimental paradigms typically use a single participant responding to pre-recorded stimuli in the confines of an fMRI scanner, which tends to limit the imitative capacity afforded by viewing and acting with the entire arm and hand. We wanted to better understand imitation as a dynamic social experience, an approach that may be essential to understand realistic imitation behaviour (Reader & Holmes, 2016). In addition, in research both with healthy individuals and apraxia patients there is little use of motion-tracking for characterising imitation in an objective fashion (with some exceptions, e.g., Braadbaart *et al*., 2012;

Campione & Gentilucci, 2011; Gold *et al.*, 2008; Hayes *et al.*, 2016, Hermsdörfer *et al.*, 1996; Krüger et al., 2014; Pan & Hamilton, 2015; Reader & Holmes, 2015; Sacheli *et al.*, 2012, 2013, 2015a, 2015b; Wild *et al.*, 2010; Williams *et al.*, 2013), despite the fact that kinematics are an important element of social interactions (Krishnan-Barman *et al.*, 2017). With this in mind, we used two-person motion-tracking in this experiment to better understand the links between actor and imitator behaviour.

To bring work on imitation in neuropsychology and healthy participants together, we used non-invasive brain stimulation to arbitrate between the roles of the two broad left IPL subregions SMG and AG in imitation, and, secondary to this, to test whether these regions are differentially involved in meaningful and meaningless action imitation. In particular, we were interested in examining both imitation accuracy and kinematics in an exploratory fashion. We applied repetitive transcranial magnetic stimulation (rTMS) to the left SMG, left AG, or during a no-rTMS baseline, then asked participants to imitate a confederate's actions in a two-person, ecologically valid and naturalistic motion-tracking paradigm.

Materials and methods

Participants

We recruited 12 participants from the University of Reading and the surrounding area (mean±SE age = 23.2±1.1 years, 5 males, 2 left handed). Left-handed participants were not excluded since, in the SMG at least, praxis representation is not related to handedness (Króliczak *et al.*, 2016). The experiment was approved by the University of Reading ethics committee (ref: UREC 15/49); participants gave written, informed consent; the experiments were conducted in accordance with the Declaration of Helsinki (as of 2008).

Stimuli and apparatus

Positions of the participant’s right arm and hand and a confederate’s left arm and hand were recorded using a Polhemus Liberty motion tracking system (Polhemus Inc., Colchester, VT, USA) recording 16 channels (8 per person) with 6 degrees of freedom (x, y, z, azimuth, elevation, and roll) at 240Hz. Trackers were attached to the shoulder (acromial end of the clavicle), elbow (olecranon), wrist (pisiform), and the thumb and finger tips, using adhesive medical tape or Velcro™. rTMS was applied using a PowerMAG 100 (Mag & More GmbH, Munich, Germany) with a 70mm figure-of-eight coil.

The experiment was controlled and data acquired using custom software written in MATLAB 2014b (Mathworks, Inc.) and using the ProkLiberty interface (https://code.google.com/p/prok-liberty/). We used LabMan and the HandLabToolbox to document and control experiments and analyse data. The associated repositories are, or will be, freely available at https://github.com/TheHandLaboratory, whilst raw data are available on request.

Thirty gestures were used as stimuli. This included five meaningful hand, five meaningful finger, and twenty matched meaningless gestures. For each meaningful gesture, two matched meaningless gestures were created. In the case of finger gestures, this was done by changing the fingers used and/or the orientation of the hand. In the case of hand gestures, this was done by changing the orientation and/or position of the hand. We used more meaningless than meaningful gestures to reduce the number of times participants were exposed to these actions, reducing the likelihood that they would associate them with a particular meaning. The finger gestures signified "okay", "thumbs up", "shoot", "peace", and "silence". The hand gestures signified "salute", "stop", "shock", "looking into the distance", and "I'm listening" (Figure 1A). Emblematic gestures were used since, unlike pantomimed actions which imply an object and require continuous motion, emblematic gestures are point-to-point which is more appropriate for motion-tracking (i.e., it is straightforward to extract a single velocity curve for analysis).

[FIGURE 1 ABOUT HERE]

During the imitation task, participants sat opposite a confederate at a round plastic table (diameter=85cm), approximately 100cm apart (Figure 1B). A Blu Tack® start point was located 20cm away from each person's abdomen. To inform the confederate of the actions they needed to perform, a computer screen (unobservable by the participant imitator) was placed parallel to the table, approximately 50cm to the left of the actor.

TMS site localisation

Visualisation of the participant’s brain used T1 weighted MR images alongside Brainsight 2.2.13 (Rogue Research Inc., Montreal, Canada). Due to SMG and AG size, stimulation locations were based on guidance from previous experimental activation and cytoarchitectonic maps (Caspers *et al.*, 2006, 2008). The stimulation site for left SMG was area PF, located by finding the dorsal extension of the posterior end of the Sylvian fissure and the anterior end of the intraparietal sulcus, drawing an imaginary line between them, and stimulating the centre of this line. Evidence suggests that area PF usually falls within these limits (Caspers *et al.* 2006). Since AG activation in neuroimaging studies of imitation appears to be less frequent than SMG activation, the stimulation site was the centre of the left AG, aiming to cover both PGa (anterior) and PGp (posterior). The AG site was located half way between the dorsal extension of the posterior superior temporal sulcus and the intraparietal sulcus. Mean±95% CI locations are shown in Figure 1C. For both AG and SMG the coil was oriented orthogonal to the main orientation of the gyrus limits. The location of the coil in the no-rTMS baseline condition was placed directly between the AG and SMG positions, but held parallel against the head, such that no or minimal stimulation of the brain should occur.

rTMS parameters

Monophasic rTMS was applied to the left SMG, left AG, and in the no-rTMS condition (coil held away from the head) at 1Hz and 110% of distance adjusted resting motor threshold (RMT, Stokes *et al.*, 2007). RMT (Rossini *et al.*, 1994) was obtained at the start of the first session. Mean±SE RMT was 69±4.1% of maximum stimulator output (MSO). The distance from M1, SMG, and AG, to the scalp was measured using Brainsight. The no-rTMS site distance was measured from the cortical tissue directly underlying the no-rTMS site to the scalp. Stimulation intensity was limited to a maximum of 85% MSO in order to prevent the coil overheating. Mean±SE stimulation intensity in each condition was as follows: SMG=70±4.1%, AG=72±4.4%, no-rTMS=71±3.9% MSO.

Design and procedure

Participants took part in three sessions split at least a week apart. On a single day rTMS was applied twice (once for meaningless, once for meaningful) for 15 minutes (900 pulses at 1Hz) to either the left SMG, left AG, or in the no-rTMS baseline condition, in counterbalanced order across participants. After each rTMS application, participants took part in either a meaningful or meaningless action imitation task. Meaningless and meaningful actions were segregated into their own separate trials (each following a single rTMS application), since there is evidence to suggest that performing novel and known actions in a sequence could recruit a single processing route, whilst presenting them separately recruits separate routes (Tessari & Rumiati, 2004; but see Press & Heyes, 2008; Reader *et al.*, under review). Task order was counterbalanced across stimulation sites.

Imitators were not given detailed instructions regarding the task constraints, and were simply told to imitate the confederate, with the aim that this would ensure naturalistic performance in the task.

Both confederate and imitator began with their thumb and forefinger gripping their start points. In both meaningful and meaningless imitation tasks, action images appearing on a computer screen (in a random order, one per trial) signalled the confederate to perform the displayed action, which they performed and maintained briefly before returning their hand to the start point. Five seconds after presentation of the image to the confederate, a tone indicated the participant to imitate the action they had observed, which they performed in a mirror fashion (i.e., using their right hand to copy the confederate's left hand). After completing the action, they returned their hand to the start point before the next trial. Following a single application of rTMS, each meaningful action was presented six times, or each meaningless action was presented three times, giving a total of 60 trials per condition and TMS site. Imitation was performed in same-sex dyads, with either a male confederate or one of two female confederates. The same confederate was used as actor for every condition of a given participant.

Following the third rTMS session, participants were presented with a questionnaire featuring the meaningful and meaningless images in pseudorandom order. They were asked to state whether they thought each gesture had a meaning and, if it did, to provide an explanation. This was done with the aim of excluding participants if they failed to meet an arbitrary 60% agreement with our meaningful and meaningless action categorisation, but no participants failed this criterion. Mean±SE agreement on the meaningful gestures was 75.8±7.83%, and the mean percentage of meaningless gestures described as meaningful was 5.83±1.83%.

Data analysis

An automated script was used for pre-processing and extraction of variables. The analysis routines processed the position data from each trial of each participant and rejected artefacts (e.g., trials with missing samples or spikes resulting from electromagnetic interference) before filtering with a bidirectional low-pass 4th order Butterworth filter (cutoff frequency 15Hz). 5.3% of trials were removed due to incorrect start times or artefacts.

The imitator's and actor's 3D velocity over their primary movement (movement onset to gesture completion, mean±SE duration=1021±34.3ms) were resampled to 240 samples then correlated in order to provide a measure of imitation accuracy (Reader & Holmes, 2015). The 3D velocity profiles for each of the imitator's trackers were correlated with each of the actor's corresponding trackers: shoulder (SH), elbow (EL), wrist (WR), thumb (TH), index finger (IN), middle finger (MI), ring finger (RI), and little finger (LI). 3D velocity profiles were used since they provide a measure of the change in the 3D position of the trackers over time, and thus the formation of the final hand posture over time. This was considered preferable to using the x, y, and z position values since it allowed us to reduce the number of statistical comparisons, and the likelihood of false positives.

In order to use parametric statistics on the resulting r-values they were converted into Z-values using Fisher's transformation ($Z=0.5*\ln((1+r)/(1-r))$), where ln is the natural logarithm. JASP (version 0.8.0.0, JASP Team) was used to perform two-way repeated measures ANOVAs on the means of all relevant trials for each of these variables across each crossed condition (Table 1). Preliminary analysis indicated that hand gestures were biasing the results (i.e., the mean Z-values for all digits were similar since the digits generally moved together). Because of this we split the hand and finger gestures before examining accuracy, then corrected for multiple comparisons using

Bonferroni correction, reducing our alpha used to determine a statistically significant result to .025. We then performed the following analysis on the hand and finger data separately.

In order to assess whether there were time-dependent significant differences in the stimulation-site related main effects or interaction, *t*-statistic plots were created to examine changes in the imitator (i.e., regardless of the actor) 3D velocity for each instance (Figure 2). We took this time-series-driven approach in order to inform us of possible differences in peak kinematic values in separate trackers, without the inflated type 1 error that would occur were we to examine multiple kinematic parameters in multiple trackers. In cases where the *t*-value was at a significant level for any sequence of samples in the time-series, we performed permutation testing on the relevant data.

Permutation testing was performed over 10,000 iterations to create a custom empirical null distribution of the length of samples with significant t-statistics, which was then used to decide whether an observed sequence was significantly long. This is similar to the use of cluster based statistics in fMRI, where a fixed, arbitrary threshold is used for creating clusters, then a second threshold is calculated for determining how large a cluster needs to be before it is statistically significant. On each iteration, the condition labels for each participant's data were pseudorandomised, and the original analyses were then repeated exactly, in order to obtain *t*-statistics, and sequences of significant *t*-statistics for the difference between 'SMG' and 'AG' conditions, under the null hypothesis. From this we were able to assign a p-value to our actual results by seeing what proportion of the tail of the distribution was greater (or lesser) than or equal to the actual result. We examined the minimum length of sequences of continuous values in which $|t|>2.201$ (i.e., statistically significant at a samplewise $p<.05$), and also the *p*-values associated with the sequences of timepoints in our recorded data where $|t|>2.201$.

Where significantly long sequences were found, we examined the standard kinematic parameters that occurred during those periods to confirm whether the differences were derived from the SMG-AG comparison, or if there was further information to be gained from the no-rTMS baseline. Imitator peak kinematic parameters were examined using one-tailed post-hoc paired *t*-tests. To check that any differences were derived from imitator rather than actor performance, we ran the same analysis on the actor peak values using two-tailed paired *t*-tests. For all post-hoc paired *t*-tests Hedges' g_{rm} was chosen to report effect sizes in repeated measures comparisons (Lakens, 2013).

Results

No significant effects of stimulation site, nor interaction between stimulation site and meaning were observed in imitation accuracy (Table 1). In hand gestures, the shoulder and elbow positions were significantly more correlated for meaningless than for meaningful actions. This effect was also significant in the same direction for the shoulder in finger gestures, and, only when uncorrected for multiple comparisons, in the elbow.

[TABLE 1 ABOUT HERE]

[FIGURE 2 ABOUT HERE]

Figure 2A shows the *t*-statistic plots for the main effect of SMG versus AG in hand gestures. Figure 2B shows the *t*-statistic plots for the interaction between stimulation site and meaning in hand gestures. Figure 2D shows the *t*-statistic plots for the interaction between stimulation site and meaning in finger gestures. No significantly long sequences were observed in these data.

Figure 2C shows the *t*-statistic plots for SMG versus AG in meaningful and meaningless actions for finger gestures. Permutation testing for the thumb revealed a significant sequence between 59 and 108 samples (*p*=.035). The index finger showed a significant sequence between 65 and 119 samples (*p*=.022). The ring finger showed a significant sequence between 72 and 116 samples (*p*=.041). The little finger showed a significant sequence between 67 and 114 samples (*p*=.036). The middle finger sequence between 70 and 106 samples was not significantly long (*p*=.054).

[FIGURE 3 ABOUT HERE]

The mean peak velocity (PV) for the digits in finger gestures was examined post-hoc since the above significant sequences overlapped with this kinematic parameter. Figure 3 emphasises this difference in the original data for the thumb. One-tailed *t*-tests for imitator mean digit PV (Figure 4) indicated a Bonferroni-corrected significant (*p*<.025) difference, where stimulation over AG resulted in a greater mean digit PV than over SMG (*t*(11)=2.23, *p*=.024, g_{rm}=0.207), and a similar difference where stimulation over AG resulted in a greater mean digit PV than the sham baseline (*t*(11)=2.10, *p*=.030, g_{rm}=0.182). There was no significant difference in mean digit PV between stimulation over SMG and the sham baseline *t*(11)=-0.503, *p*=.303, g_{rm}=0.0465).

We then used two-tailed *t*-tests to perform the same analysis on the PV of the *actor* in their finger gestures (Figure 4), which revealed a Bonferroni-corrected significant (p<.025) difference between mean digit PV in the AG condition and sham baseline (*t*(11)=2.91, *p*=.014, g_{rm}=0.529). There was no significant difference in mean digit PV following stimulation over SMG and the sham baseline (*t*(11)=1.89, *p*=.086, g_{rm}=0.331), or between SMG and AG conditions (*t*(11)=-1.71, *p*=.115, g_{rm}=0.222). This suggested that actor behaviour was biased, so we also decided post-hoc to examine the imitator PV relative to the actor PV to try and control for the effects of this bias.

[FIGURE 4 ABOUT HERE]

We examined the imitator mean digit PV relative to the actor mean digit PV in finger gestures using two-tailed *t*-tests and a Bonferroni-corrected alpha criterion of .025 (Figure 5). There were no significant differences using this corrected criterion. However, mean digit relative PV was reduced following SMG stimulation compared to the sham baseline ($t(11)=-2.37$, $p=.037$, $g_{rm}=0.335$), and also following AG stimulation compared to the sham baseline ($t(11)=-2.31$, $p=.041$, $g_{rm}=0.281$). There was also no significant difference in mean digit relative PV between SMG and AG stimulation ($t(11)=-0.316$, $p=.758$, $g_{rm}=0.0424$).

[FIGURE 5 ABOUT HERE]

Discussion

We tested participants' ability to imitate meaningful and meaningless hand and finger gestures following rTMS over the left SMG, left AG, or after a no-rTMS baseline. Whilst there were no differences in imitation accuracy between stimulation sites, we observed that participants' digit peak velocity was lower relative to the actor in finger gestures following left SMG or left AG stimulation, though with a larger effect size in the SMG condition. These results provide the first causal evidence, using brain stimulation in healthy individuals, for a role of the left IPL in processing the kinematics of finger movements during gesture imitation.

Whilst stimulation did not influence imitation accuracy, there was some evidence for differences between accuracy in meaningful and meaningless action performance. Interestingly, participants matched the confederate's shoulder and elbow movements to a significantly greater degree in meaningless actions. Meaningless actions may rely more on matching action kinematics (e.g., Rumiati & Tessari, 2002; Tessari & Rumiati, 2004; Wild *et al.*, 2010) than meaningful actions. The fact that effects were only observed in the shoulder and elbow may reflect the fact that the differences in accuracy were easier to detect in proximal effectors with lower degrees of freedom.

Examining *t*-statistics over time, we found significantly long periods during which imitator finger velocity was significantly lower following rTMS over left SMG compared to left AG during imitation of finger gestures, but regardless of action meaning. This effect was also reflected in mean digit PV. To account for possible differences in actor behaviour, we examined imitator mean digit PV relative to the actor mean digit PV, and found that participants showed significantly reduced mean digit PV relative to the actor following SMG and AG stimulation compared to baseline. This result seems to indicate that during the imitation of finger gestures, rTMS to the left SMG or left AG reduces digit velocity relative to the observed actor. Further study is necessary to understand the underlying processes altered in this experiment, but these results have the potential to bring together both findings from apraxia and discussions of the putative mirror neuron system in healthy individuals.

As noted in the introduction, some suggest that the putative human mirror neuron system supports our imitative capacity. The IPL is one area of this proposed frontoparietal system (Hamilton, 2015), that has been suggested to support imitation through visuomotor matching of seen actions and those that are already in the motor repertoire. This theory provides one explanation for our result in the absence of any stimulation-related effects specific to action meaning. That is, disturbed visuomotor matching following stimulation over left IPL could reduce the velocity with which the fingers shape complex postures relative to the actor. However, this effect does not necessarily stem from an rTMS-induced inhibition of direct matching. Rather, by considering claims made in the mirror neuron literature and neuroimaging studies of healthy individuals, recent discussions in apraxia, and recognising the possibility that different areas of the IPL may subserve different aspects of imitation, we may be able to provide a more holistic explanation for the observed data.

Buxbaum *et al.* (2014) found that damage to the left IPL was associated with deficits in kinematic (rather than postural) aspects of movement for novel and tool-related actions. Similar results were found in a more recent voxel-based lesion-symptom mapping study by Dressing *et al.* (2016). Buxbaum *et al.* (2014) suggested that the left IPL computes "movement plans [as] dynamic changes in the relative spatial positions of body parts needed to reach a goal configuration" (p. 13). If this is the case, changes in effector movement relative to the goal (the actor movement) are a possible consequence of left IPL stimulation. Our results indicate that this is true for both intransitive meaningful and meaningless actions. Whilst meaningless action imitation may be *more* reliant on kinematic processing (Buxbaum *et al.*, 2014), kinematic information might still be relevant to the way in which one must replicate a meaningful action. To take an extreme example, the imitator is not likely to ignore explicit but irrelevant kinematics, such as a particularly slow or rapid action which does not assist in the development of the final posture (see Forbes & Hamilton, 2017, for evidence that possibly supports this).

Our results seem, then, to confirm the importance of the left IPL in meeting the kinematic requirements of the observed action, over and above the meaning of that action. The sensitivity of the IPL to observed movement kinematics (Becchio *et al.*, 2012) might substantiate this claim, and since movement necessarily contains kinematic features, our results may help to explain why left IPL activity is frequently reported during imitation in healthy individuals, regardless of the type of action imitated (e.g., Jack *et al.*, 2011; Molenberghs *et al.*, 2010; Mühlau *et al.*, 2005; Tanaka *et al.*, 2002). There is also evidence, at least for tool-related actions, that damage to the left IPL is more reliably associated with deficits in action performance, rather than action recognition (Tarhan *et al.*, 2015), potentially confirming the priority that the left IPL places on processing movement during imitation, rather than semantic encoding (which may be more reliably served by the temporal lobe e.g., Dressing *et al.*, 2016; Kalénine *et al.*, 2010).

It is worth stressing here that our assertion is made in the light of our use of intransitive emblematic gestures, whilst the term 'meaningful gesture' in apraxia literature commonly refers to action pantomimes (i.e., pretending to perform a tool-use hand action without the tool in hand). A more detailed discussion of the distinctions between object-directed and emblematic gestures is provided by Buxbaum *et al.*, 2005. However, there is evidence that damage to the IPL can be associated with deficits in both the imitation of communicative and tool-use gestures (e.g., Dressing *et al.*, 2016), implying that our findings may be applicable beyond the specific action types used in this experiment. We do, of course, suggest further testing this hypothesis.

It is also worth noting that the size of the IPL indicates that it is not solely involved in the kinematic matching process we have proposed. Indeed, this was part of our motivation for using cytoarchitectonically defined brain regions for stimulation. It is perhaps more feasible that the left parietal lobe is involved in multiple processes for imitation, and that these processes may be dependent on the type of action to be imitated. For example, the parietal operculum (POp), anterior to area PF, or the anterior intraparietal sulcus (aIPS), superior to area PF, have also been found to be involved in imitation. Specifically, some have suggested that during imitation the left POp is involved in comparing information about the imitator's body with the observed actor's body (Krüger *et al.*, 2014; Mengotti *et al.*, 2013), and that activity in this area is correlated with the subsequent accuracy of the imitative action (Krüger *et al.*, 2014). The left aIPS, however, has been suggested to guide object-directed hand movements (Tunik *et al.*, 2007) and, importantly, also appears to represent the goals of observed object-directed actions (Hamilton, 2008, 2014; Hamilton

& Grafton, 2006, 2007; Sacheli *et al*., 2015). As such, the aIPS could support the imitation of object-directed actions because it ostensibly provides a “common representational system for the actions of self and other” (p. T84, Tunik *et al*., 2007). The sensitivity of the aIPS for both observed and performed action goals (Oosterhof *et al*., 2010) is in keeping with claims that this area may be part of the putative human mirror neuron system (Tunik *et al*., 2007). Lastly, Goldenberg & Randerath (2015) suggested that the left IPL could have a role in the apprehension of spatial relationships. They report that damage to this area can result in shared deficits in the imitation of meaningless hand gestures, which require placing the hand in relation to other parts of the body whilst the finger positions remain invariant, and in tasks such as the Token Test which require patients to classify objects based on their spatial and physical properties.

With the above in mind we can distinguish four potential elements of imitation served by the left parietal lobe. Left area PF and/or area PG - the parts of the SMG and AG stimulated in this experiment - could be involved in creating movement plans based on the spatiotemporal requirements of the to-be-performed action (i.e., the kinematics), regardless of whether the action is imitative. The POp could then ensure that these spatiotemporal requirements are met during imitative scenarios, by comparing the imitator’s body to that of the actor (Krüger *et al*., 2014; Mengotti *et al*., 2013). This checking process may be essential for meaningless intransitive actions, in the absence of objects to provide context, and could provide one explanation for the defective imitation of meaningless gestures frequently associated with left IPL damage (Goldenberg, 2009). The aIPS, in contrast, could be useful for informing imitation in object-directed scenarios (but see Martin *et al*., 2016), where visuomotor matching between the observed and to-be-performed action can be done at the goal rather than movement level (Hamilton, 2014). There may also be a role for the left IPL in processing spatial relationships during imitation. This may be particularly important for the imitation of meaningless hand gestures (Goldenberg & Karnath, 2006; Goldenberg & Randerath, 2015), since this task could be reliant on the decomposition of visual information about the observed gesture into “simple spatial relationships between a limited number of defined body parts” (p. 47, Goldenberg & Randerath, 2015). The absence of specific effects for meaningless hand gesture imitation in our experiment is discussed later.

In light of the discussion above, it is also necessary for us to comment on the similar effects observed for both of our active stimulation sites. Unfortunately, our study was not able to reveal more about the possible division of labour between the left SMG and AG. The existence of similar effects in both the left SMG and AG may not necessarily reflect similar roles for each of these regions, but perhaps the connectivity between them. For example, the left AG stimulation may have had an effect on information processing between the AG and SMG, with the greater effect size observed following SMG stimulation (Hedges’ g_{rm} = 0.335 versus 0.281) partially supportive of this claim. Since the AG is anatomically connected to the posterior SMG (Seghier, 2013), rTMS over both areas might induce a reduction in efficient SMG functioning if information regarding the kinematic constraints of the observed action is passed in a posterior-anterior (AG to SMG) fashion. It is also worth noting that a previous study indicated that the AG could be involved in both meaningful and meaningless action imitation (Vanbellingen *et al.*, 2014). However, the location of AG in that experiment was more ventral and anterior to ours.

An alternative explanation for the similar effects observed for both stimulation sites is that our results reflect an influence of unspecified peripheral stimulation of another area of the IPL, for example, cytoarchitectonic area PFm, which lies between PF (in the SMG) and PGa (AG). Interestingly, a previous study by Weiss *et al.* (2013) using transcranial direct current stimulation (tDCS), found that anodal stimulation over left area PFm improved participants’ gesture matching ability. However, the authors suggested that their result could have been driven by a combined effect of SMG and AG stimulation, considering the central position of PFm, and the size of tDCS electrodes. Weiss *et al.* (2013) stated that both parts of the IPL may have to be stimulated simultaneously in order to facilitate gesture matching. Considering our results, the same could be true for influencing gesture imitation, and further highlights the importance of considering in detail the role of different regions of the IPL, along with their interactions.

One response to this problem is to suggest further neurostimulation research aimed at disentangling the relative contributions of the seven parcellated regions of the IPL (PFt, PFop [the POp], PFcm, PF, PFm, PGa, PGp), along with the aIPS. Such an endeavour would be essential in order to clarify how different areas of the left parietal lobe may or may not interact, and their relative contributions to different types of action and action imitation. In addition, neuroimaging approaches that compare brain activity with actual imitative performance (i.e., Frey & Gerry, 2006; Krüger *et al*., 2014), across different types of action, are also likely to be invaluable. In general we suggest that, where possible, researchers try to report in more detail at least the distinction between the SMG and AG, if not their parcellated subregions, rather than stating a role for the IPL in general.

A potential limitation of this study, and another possible explanation for the consistent effects observed in both the SMG and AG, is that these results simply reflect a TMS-general influence, in the absence of an active control site. TMS can cause changes in behaviour distinctly unrelated to changes in cortical activity, whereby the clicking sound of the TMS coil alone can facilitate or inhibit reaction times dependent on the time of stimulation within a trial (Duecker *et al*., 2013; Meteyard & Holmes, 2018). However, as far as we are aware this has only been found for online TMS protocols, and we are not aware of data suggesting that the offline approach we used is also likely to result in ‘mere-presence’ effects of rTMS. In addition, the no-rTMS session involved much of the same conditions as in the active stimulation sessions (e.g., 15 minutes of waiting during TMS application, clicking sound).

Finally, it is interesting that our primary result was found specifically for finger gestures, rather than hand gestures. This is partly at odds with some previous findings in apraxia, though our stimuli were not modelled on previous distinctions between hand and finger gestures – our main aim was to ensure there was a sufficient number of different emblematic stimuli for participants to copy. There is some evidence to suggest that defective finger gesture imitation is more associated with left inferior frontal gyrus damage, compared to defective hand gesture imitation, which is more associated with left IPL damage (Goldenberg & Karnath, 2006). As stated above, some discuss the role of the left IPL in hand gesture imitation in terms of 'body part coding', where hand gesture imitation is reliant on the spatial mapping of the hand in relation to other body parts (e.g., Goldenberg & Karnath, 2006; Goldenberg & Randerath, 2015). However, some experimenters have failed to find a dissociation for brain regions related to defective hand and finger imitation (Achilles *et al*., 2017). It is also possible that the movement to attain the posture, rather than the final hand position alone may be an important factor. For example, whilst the Goldenberg (1996) assessment for meaningless gestures (as used by Goldenberg & Karnath, 2006 and Goldenberg & Randerath, 2015) considers only performance on the final gesture posture, Buxbaum *et al.* (2014) examined dynamic movements, hence their suggestion that dynamic change in body part position is important. It is possible that the difference between kinematic and postural elements of movement may take precedence over the difference between hand and finger gestures, though further research would be needed to clarify this. If this is the case, the fact we only observed kinematic effects in the finger velocities for finger-specific gestures may reflect the fact that the dynamic change of each of the fingers independently is more complex than the movement of the hand as a whole.

In conclusion, we found that the left IPL is involved in matching observed digit velocity in action imitation, regardless of action meaning. More work is needed to expand on how imitation kinematics are processed in the left IPL, and the relative contributions of the SMG and AG and their respective cytoarchitectonic subregions. These nuances can be examined using neuronavigated TMS. Our results highlight that brain stimulation may help close the gap in understanding imitation in apraxia and in healthy people, particularly if it is combined with large-scale motion-tracking.

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Conflict of interest statement

The authors report no conflict of interest.

Author contributions

All authors have made significant contributions to this article. In particular, experiment design, analysis, and manuscript writing by ATR and NPH, proofing by ATR, BPR, JEM, KC, and NPH, and participant recruitment and data collection by ATR, BPR, JEM, and KC.

Data accessibility statement:

Raw data and analysis scripts are freely available from the corresponding author (ATR).

Abbreviations

AG: angular gyrus

aIPS: anterior intraparietal sulcus

IPL: inferior parietal lobule

MF: meaningful

ML: meaningless

POp: parietal operculum

rTMS: repetitive transcranial magnetic stimulation

SMG: supramarginal gyrus

References

Achilles, E.I.S., Weiss, P.H., Fink, G.R., Binder, E., Price, C.J., & Hope, T.M.H. (2017). Using multi-level Bayesian lesion-symptom mapping to probe the body-part-specificity of gesture imitation skills. *NeuroImage*, **161**, 94-103. doi:10.1016/j.neuroimage.2017.08.036

Bien, N., Roebroeck, A., Goebel, R., & Sack, A.T. (2009). The brain's intention to imitate: the neurobiology of intentional versus automatic imitation. *Cereb. Cortex*, **19**, 2338-2351. doi:10.1093/cercor/bhn251

Becchio, C., Cavallo, A., Begliomini, C., Sartori, L., Feltrin, G., & Castiello, U. (2012). Social grasping: From mirroring to mentalizing. *NeuroImage*, **61**, 240-248. doi:10.1016/j.neuroimage.2012.03.013

Braadbaart, L., Waiter, G.D., & Williams, J.H.G. (2012). Neural correlates of individual differences in manual imitation fidelity. *Front. Integr. Neurosci.*, **6**, 91. doi:10.3389/fnint.2012.00091

Buxbaum, L.J., Kyle, K.M., & Menon, R. (2005). On beyond mirror neurons: internal representations subserving imitation and recognition of skilled object-related actions in humans. *Cog. Brain Res.*, **25**, 226-239. doi:10.1016/j.cogbrainres.2005.05.014

Buxbaum, L.J., Shapiro, A.D., & Coslett, H.B. (2014). Critical brain regions for tool-related and imitative actions: a componential analysis. *Brain*, **137**, 1971-1985. doi:10.1093/brain/awu111

Campione, G.C., & Gentilucci, M. (2011). Is the observation of the human kinematics sufficient to activate automatic imitation of transitive actions? *Behav. Brain Res.*, **225**, 201-208. doi:10.1016/j.bbr.2011.07.025

Carmo, J.C., Rumiati, R.I., & Vallesi, A. (2012). Understanding and imitating unfamiliar actions: distinct underlying mechanisms. *PLOS ONE*, 7, e46939. doi:10.1371/journal.pone.0046939

Caspers, S., Geyer, S., Schleicher, A., Mohlberg, H., Amunts, K., & Zilles, K. (2006). The human inferior parietal cortex: Cytoarchitectonic parcellation and interindividual variability. *NeuroImage*, **33**, 430-448. doi:10.1016/j.neuroimage.2006.06.054

Caspers, S., Eickhoff, S.B., Geyer, S., Scheperjams, F., Mohlberg, H., Zilles, K., & Amunts, K. (2008). The human inferior parietal lobule in stereotaxic space. *Brain Struct. Func.*, **212**, 481-495. doi:10.1007/s00429-008-0195-z

Caspers, S., Zilles, K., Laird, A.R., & Eickhoff, S.B. (2010). ALE meta-analysis of action observation and imitation in the human brain. *NeuroImage*, **50**, 1148-1167. doi:10.1016/j.neuroimage.2009.12.112

Decety, J., Grèzes, J., Costes, N., Perani, D., Jeannerod, M., Procyk, E., Grassi, F., & Fazio, F. (1997). Brain activity during observation of actions: influence of action content and subject's strategy. *Brain*, **120**, 1763-1777.

Dressing, A., Nitschke, K., Kümmerer, D., Bormann, T., Beume, L., Schmidt, C.S.M., Ludwig, V.M., Mader, I., Willmes, K., Rijntjes, M., Kaller, C.P., Weiller, C., & Martin, M. (2016). Distinct contributions of dorsal and ventral streams to imitation of tool-use and communicative gestures. *Cereb. Cortex*. doi:10.1093/cercor/bhw383

Duecker, F., de Graaf, T.A., Jacobs, C., & Sack, A.T. (2013). Time- and task-dependent non-neural effects of real and sham TMS. *PLOS ONE*, **8**, e73813. doi:10.1371/journal.pone.0073813

Forbes, P.A.G., & Hamilton, A.F. de C. (2017). Moving higher and higher: imitators' movements are sensitive to observed trajectories regardless of action rationality. *Exp. Brain Res*. doi:10.1007/s00221-017-5006-4

Frey, S.H., & Gerry, V.E. (2006). Modulation of neural activity during observational learning of actions and their sequential orders. *J. Neurosci*., **26**, 13194-13201. doi:10.1523/JNEUROSCI.3914-06.2006

Gold, B.J., Pomplun, M., Rice, N.J., & Sekuler, R. (2008). A new way to quantify the fidelity of imitation: preliminary results with gesture sequences. *Exp. Brain Res.*, **187**, 139-152. doi:10.1007/s00221-008-1291-2

Goldenberg, G. (1996). Defective imitation of gestures in patients with damage in the left or right hemispheres. *J. Neurol. Neurosurg. Psychiatry*, **61**, 176-180.

Goldenberg, G. (2009). Apraxia and the parietal lobes. *Neuropsychologia*, **47**, 1449-1459. doi:10.1016/j.neuropsychologia.2008.07.014

Goldenberg, G., & Karnath, H. (2006). The neural basis of imitation is body part specific. *J. Neurosci.*, **26**, 6282-6287. doi:10.1523/JNEUROSCI.0638-06.2006

Goldenberg, G., & Randerath, J. (2015). Shared neural substrates of apraxia and aphasia. *Neuropsychologia*, **75**, 40-49. doi:10.1016/j.neuropsychologia.2015.05.017

Grèzes, J. (1998). Top down effect of strategy on the perception of human biological motion: a pet investigation. *Cogn. Neuropsychol.*, **15**, 553-582. doi:10.1080/026432998381023

Hamilton, A.F. de C. (2008). Emulation and mimicry for social interaction: A theoretical approach to imitation in autism. *Q. J. Exp. Psychol.*, **61**, 101-115. doi:10.1080/17470210701508798

Hamilton, A.F. de C. (2014). Cognitive underpinnings of social interaction. *Q. J. Exp. Psychol.*, **68**, 417-412. doi:10.1080/17470218.2014.973424

Hamilton, A.F. de C. (2015). The neurocognitive mechanisms of imitation. *Curr. Opin. Behav. Sci.*, **3**, 63-67. doi:10.1016/j.cobeha.2015.01.011

Hamilton, A.F. de C., & Grafton, S.T. (2006). Goal representation in human anterior intraparietal sulcus. *J. Neurosci.*, **26**, 1133-1137. doi:10.1523/JNEUROSCI.4551-05.2006

Hamilton, A.F. de C., & Grafton, S.T. (2007). The motor hierarchy: from kinematics to goals and intentions. In Rosetti, Y., Kawato, M., & Haggard, P. (eds), *Attention & Performance 22*. Oxford University Press, Oxford.

Hayes, S.J., Dutoy, C.A., Elliott, D., Gowen, E., & Bennett, S.J. (2016). Atypical biological motion kinematics are represented by complementary lower-level and top-down processes during imitation learning. *Acta Psychol.*, **163**, 10-16. doi:10.1016/j.actpsy.2015.10.005

Hermsdörfer, J., Mai, N., Spatt, J., Marquardt, C., Veltkamp, R., & Goldenberg, G. (1996). Kinematic analysis of movement imitation in apraxia. *Brain*, **119**, 1575-1586.

Higuchi, S., Holle, H., Roberts, N., Eickhoff, S.B., & Vogt, S. (2012). Imitation and observational learning of hand actions: prefrontal involvement and connectivity. *NeuroImage*, **59**, 1668-1683. doi:10.1016/j.neuroimage.2011.09.021

Iacoboni, M. (2009). Imitation, empathy, and mirror neurons. *Annu. Rev. Psychol.*, **60**, 653-670. doi:10.1146/annurev.psych.60.110707.163604

Iacoboni, M., & Dapretto, M. (2006). The mirror neuron system and the consequences of its dysfunction. *Nat. Rev. Neurosci.*, **7**, 942-951. doi:10.1038/nrn2024

Jack, A., Englander, Z.A., & Morris, J.P. (2011). Subcortical contributions to effective connectivity in brain networks supporting imitation. *Neuropsychologia*, **49**, 3689-3698. doi:10.1016/j.neuropsychologia.2011.09.024

Kalénine, S., Buxbaum, L.J., & Coslett, H.B. (2010). Critical brain regions for action recognition: lesion symptom mapping in left hemisphere stroke. *Brain*, **133**, 3269-3280. doi:10.1093/brain/awq210

Koski, L., Iacoboni, M., Dubeau, M., Woods, R.P., & Mazziotta, J.C. (2003). Modulation of cortical activity during different imitative behaviors. *J. Neurophysiol.*, **89**, 460-471. doi:10.1152/jn.00248.2002

Krishnan-Barman, S., Forbes, P.A.G., & Hamilton, A.F. de C. (2017). How can the study of action kinematics inform our understanding of human social interaction? *Neuropsychologia*, **105**, 101-110. doi: 10.1016/j.neuropsychologia.2017.01.018

Króliczak, G., Piper, B.J., & Frey, S.H. (2016). Specialization of the left supramarginal gyrus for hand-independent praxis representation is not related to hand dominance. *Neuropsychologia*, **93**, 501-512. doi:10.1016/j.neuropsychologia.2016.03.023.

Krüger, B., Bischoff, M., Blecker, C., Langhanns, C., Kindermann, S., Sauerbier, I., Reiser, M., Stark, R., Munzert, J., & Pilgramm, S. (2014). Parietal and premotor cortices: Activation reflects imitation accuracy during observation, delayed imitation and concurrent imitation. *NeuroImage,* **100**, 39-50. doi:10.1016/j.neuroimage.2014.05.074

Lakens, D. (2013). Calculating and reporting effect sizes to facilitate cumulative science: a practical primer for *t*-tests and ANOVAs. *Front. Psychol.,* **4**, 863. doi:10.3389/fpsyg.2013.00863

Martin, M., Nitschke, K., Beume, L., Dressing, A., Bühler, L.E., Ludwig, V.M., Mader, I., Rijntjes, M., Kaller, C.P., & Weiller, C. Brain activity underlying tool-related and imitative skills after major left hemisphere stroke. *Brain*, **139**, 1497-1516. doi:10.1093/brain/aww035

Menz, M.M., McNamara, A., Klemen, J., & Binkofski, F. (2009). Dissociating networks of imitation. *Hum. Brain Mapp.*, **30**, 3339-3350. doi:10.1002/hbm.20756

Mengotti, P., Ticini, L.F., Waszak, F., Schütz-Bosbach, S., & Rumiati, R.I. (2013). Imitating others' actions: transcranial magnetic stimulation of the parietal opercula reveals the processes underlying automatic imitation. *Eur. J. Neurosci*. **37**, 316–322. doi:10.1111/ejn.12019

Meteyard, L., & Holmes, N.P. (under review) TMS SMART – scalp mapping of annoyance ratings and twitches caused by transcranial magnetic stimulation. *J. Neurosci. Meth.*

Molenberghs, P., Brander, C., Mattingley, J.B., & Cunnington, R. (2010). The role of the superior remporal sulcus and the mirror neuron system in imitation. *Hum. Brain Mapp.*, **31**, 1316-1326. doi:10.1002/hbm.20938

Molenberghs, P., Cunnington, R., & Mattingley, J.B. (2009). Is the mirror neuron system involved in imitation? A short review and meta-analysis. *Neurosci. Biobehav. Rev.*, **33**, 975-980. doi:10.1016/j.neubiorev.2009.03.010

Mühlau, M., Hermsdörfer, J., Goldenberg, G., Wohlschläger, A.M., Castrop, F., Stahl, R., Röttinger, M., Erhard, P., Haslinger, B., Ceballos-Baumann, A.O., Conrad, B., & Boecker, H. (2005). Left inferior parietal dominance in gesture imitation: an fMRI study. *Neuropsychologia*, **43**, 1086-1098. doi:10.1016/j.neuropsychologia.2004.10.004

Oosterhof, N.N., Wiggett, A.J., Diedrichsen, J., Tipper, S.P., & Downing, P.E. (2010). Surface-based information mapping reveals crossmodal vision–action representations in human parietal and occipitotemporal cortex. *J. Neurophysiol.*, **104**, 1077-1089. doi:10.1152/jn.00326.2010

Pan, X., & Hamilton, A.F. de C. (2015). Automatic imitation in a rich social context with virtual characters. *Front. Psychol.*, **6**, 790. doi:10.3389/fpsyg.2015.00790

Press, C., & Heyes, C. (2008). Stimulus-driven selection of routes to imitation. *Exp. Brain Res.*, **188**, 147-152. doi:10.1007/s00221-008-1422-9

Reader, A.T., & Holmes, N.P. (2015). Video stimuli reduce object-directed imitation accuracy: a novel two-person motion-tracking approach. *Front. Psychol.*, **6,** 644. doi:10.3389/fpsyg.2015.00644

Reader, A.T., & Holmes, N.P. (2016). Examining ecological validity in social interaction: problems of visual fidelity, gaze, and social potential. *Culture and Brain*, **4**, 134-146. doi:10.1007/s40167-016-0041-8

Rizzolatti, G., Cattaneo, L., Fabbri-Destro, M., & Rozzi, S. (2014). Cortical mechanisms underlying the organization of goal-directed actions and mirror neuron-based action understanding. *Physiol. Rev.*, **94**, 655-706. doi:10.1152/physrev.00009.2013.

Rossini, P.M., Barker, A.T., Berardelli, A., Caramia, M.D., Caruso, G., Cracco, R.Q., Dimitrijević, M.R., Hallett, M., Katayama, Y., Lücking, C.H., et al. (1994). Non-invasive electrical and magnetic stimulation of the brain, spinal cord and roots: basic principles and procedures for routine clinical application. Report of an IFCN committee. *Electroencephalogr. Clin. Neurophysiol.*, **91**, 79-92.

Rumiati, R.I., & Tessari, A. (2002). Imitation of novel and well-known actions: the role of short term memory. *Exp. Brain Res.*, **142**, 425-433. doi:10.1007/s00221-001-0956-x

Rumiati, R.I., Weiss, P.H., Tessari, A., Assmus, A., Zilles, K., Herzog, H., & Fink, G.R. (2005). Common and differential neural mechanisms supporting imitation of meaningful and meaningless actions. *J. Cognitive Neurosci.*, **17**, 1420-1431.

Sacheli, L.M., Candidi, M., Pavone, E.F., Tidoni, E., & Aglioti, S.M. (2012). And yet they act together: interpersonal perception modulates visuo-motor interference and mutual adjustments during a joint-grasping task. *PLOS ONE*, **7**, e50223. doi:10.1371/journal.pone.0050223

Sacheli, L.M., Tidoni, E., Pavone, E.F., Aglioti, S.M., & Candidi, M. (2013). Kinematics fingerprints of leader and follower role-taking during cooperative joint actions. *Exp. Brain Res.*, **226**, 473-486. doi:10.1007/s00221-013-3459-7

Sacheli, L.M., Candidi, M., Era, V., & Aglioti, S.M. (2015). Causative role of left aIPS in coding shared goals during human–avatar complementary joint actions. *Nat. Commun.*, **6**, 7544. doi:10.1038/ncomms8544

Sacheli, L.M., Christensen, A.., Giese, M.A., Taubert, N., Pavone, E.F., Aglioti, S.M., & Candidi, M. (2015b). Prejudiced interactions: implicit racial bias reduces predictive simulation during joint action with an out-group avatar. *Sci. Rep.*, **5**, 8507. doi:10.1038/srep08507

Seghier, M.L. (2013). The angular gyrus: multiple functions and multiple subdivisions. *The Neuroscientist*, **19**, 43-61. doi:10.1177/1073858412440596

Stokes, M.G., Chambers, C.D., Gould, I.C., English, T., McNaught, E., McDonald, O., & Mattingley, J.B. (2007). Distance-adjusted motor threshold for transcranial magnetic stimulation. *Clin. Neurophysiol.*, **118**, 1617-1625. doi:10.1016/j.clinph.2007.04.004

Tanaka, S., Inui, T., Iwaki, S., Konishi, J., & Nakai, T. (2001). Neural substrates involved in imitating finger configurations: an fMRI study. *NeuroReport*, **12**, 1171-1174.

Tanaka, S., & Inui, T. (2002). Cortical involvement for action imitation of hand/arm postures versus finger configurations: an fMRI study. *NeuroReport*, **13**, 1599-1602.

Tarhan, L.Y., Watson, C.E., & Buxbaum, L.J. (2015). Shared and distinct neuroanatomic regions critical for tool-related action production and recognition: evidence from 131 left-hemisphere stroke patients. *J. Cogn. Neurosci.*, **27**, 2491-2511. doi:10.1162/jocn_a_00876

Tessari, A., & Rumiati, R.I. (2004). The strategic control of multiple routes in imitation of actions. *J. Exp. Psychol.-Hum. Percept. Perform.*, **30**, 1107-1116. doi:10.1037/0096-1523.30.6.1107

Tunik, E., Rice, N.J., Hamilton, A., & Grafton, S.T. (2007). Beyond grasping: representation of action in human anterior intraparietal sulcus. *NeuroImage*, **36**, T77-T86. doi:10.1016/j.neuroimage.2007.03.026

Vanbellingen, T., Berschi, M., Nyffler, T., Cazzoli, D., Wiest, R., Bassetti, C., Kaelin-Lang, A., Müri, R., & Bohlhalter, S. (2014). Left posterior parietal theta burst stimulation affects gestural imitation regardless of semantic content. *Clin. Neurophysiol.*, **125**, 457-462. doi:10.1016/j.clinph.2013.07.024

Weiss, P.H., Achilles, E.I.S., Moos, K., Hesse, M.D., Sparing, R., & Fink, G.R. (2013). Transcranial direct current stimulation (tDCS) of left parietal cortex facilitates gesture processing in healthy subjects. *J. Neurosci.*, **33**, 19205-19211. doi:10.1523/JNEUROSCI.4714-12.2013

Wild, K.S., Poliakoff, E., Jerrison, A., & Gowen, E. (2010). The influence of goals on movement kinematics during imitation. *Exp. Brain Res.*, **204**, 353-360. doi:10.1007/s00221-009-2034-8

Williams, J.H.G., Casey, J.M., Braadbaart, L., Culmer, P.R., & Mon-Williams, M. (2013). Kinematic measures of imitation fidelity in primary school children. *J. Cogn. Dev.*, **15**, 345-362. doi:10.1080/15248372.2013.771265

Table 1: Two-way ANOVA main effects and interactions for actor-imitator correlations (*Z*-values) in hand and finger gestures; significant *p*-values (<.025) are in bold; SH: shoulder, EL: elbow, WR: wrist, TH: thumb, IN: index finger, MI: middle finger, RI: ring finger, LI: little finger

Gesture	Tracker	Mean(±SE) Z-value					Main effect						Site*meaning interaction		
		Site			Meaning		Site			Meaning			*F* (2,22)	*p*	η_p^2
		SMG	AG	No-rTMS	MF	ML	*F* (2,22)	*p*	η_p^2	*F* (1,11)	*p*	η_p^2			
Hand	SH	0.504 (0.0725)	0.485 (0.0687)	0.525 (0.0534)	0.388 (0.0514)	0.622 (0.0669)	0.243	.787	.022	39.2	**<.001**	.781	2.84	.080	.205
	EL	0.906 (0.0930)	0.860 (0.0989)	0.918 (0.0708)	0.753 (0.0862)	1.04 (0.0679)	0.253	.779	.022	28.8	**<.001**	.723	1.48	.250	.118
	WR	1.54 (0.0833)	1.57 (0.0740)	1.50 (0.0673)	1.54 (0.0658)	1.53 (0.0822)	1.07	.359	.089	0.051	.826	.005	0.256	.777	.023
	TH	1.54 (0.0760)	1.53 (0.0835)	1.52 (0.0646)	1.53 (0.0730)	1.53 (0.0708)	0.076	.927	.007	0.002	.966	<.001	0.905	.419	.076
	IN	1.48 (0.0861)	1.50 (0.0772)	1.49 (0.0650)	1.48 (0.0766)	1.50 (0.0686)	0.045	.956	.004	0.263	.618	.023	0.696	.509	.060
	MI	1.53 (0.0845)	1.52 (0.0744)	1.52 (0.0615)	1.51 (0.0750)	1.54 (0.0638)	0.004	.997	<.001	0.322	.582	.028	0.698	.508	.060
	RI	1.53 (0.0830)	1.52 (0.0738)	1.52 (0.0616)	1.51 (0.0743)	1.53 (0.0621)	0.027	.974	.002	0.173	.685	.015	0.694	.510	.059
	LI	1.52 (0.0854)	1.52 (0.0749)	1.52 (0.0624)	1.52 (0.0769)	1.52 (0.0648)	0.011	.989	.001	0.014	.909	.001	0.620	.547	.053
Finger	SH	0.122 (0.0328)	0.119 (0.0398)	0.112 (0.0280)	0.0486 (0.0309)	0.187 (0.0277)	0.040	.961	.004	37.1	**<.001**	.771	0.099	.906	.009
	EL	0.460 (0.0845)	0.492 (0.112)	0.359 (0.0683)	0.386 (0.0791)	0.488 (0.0710)	1.14	.337	.094	6.54	.027	.373	2.03	.155	.156
	WR	1.30 (0.0786)	1.34 (0.0603)	1.21 (0.0633)	1.31 (0.0594)	1.25 (0.0694)	3.19	.061	.225	1.95	.190	.151	1.33	.285	.108
	TH	1.27 (0.0538)	1.31 (0.0671)	1.20 (0.0553)	1.30 (0.0614)	1.23 (0.0469)	2.18	.137	.165	2.27	.160	.171	0.045	.956	.004
	IN	1.18 (0.0563)	1.24 (0.0701)	1.14 (0.0610)	1.20 (0.0654)	1.17 (0.0495)	1.53	.239	.122	.579	.463	.050	0.739	.489	.063
	MI	1.22 (0.0521)	1.31 (0.0516)	1.19 (0.0513)	1.28 (0.0507)	1.20 (0.0403)	2.85	.079	.206	3.43	.091	.238	.088	.916	.008
	RI	1.25 (0.0604)	1.31 (0.0511)	1.19 (0.0506)	1.27 (0.0540)	1.23 (0.0414)	2.77	.085	.201	1.17	.303	.096	0.594	.561	.051
	LI	1.23 (0.0576)	1.31 (0.0595)	1.18 (0.0487)	1.28 (0.0536)	1.20 (0.0421)	2.90	.076	.208	6.45	.028	.370	0.772	.474	.066

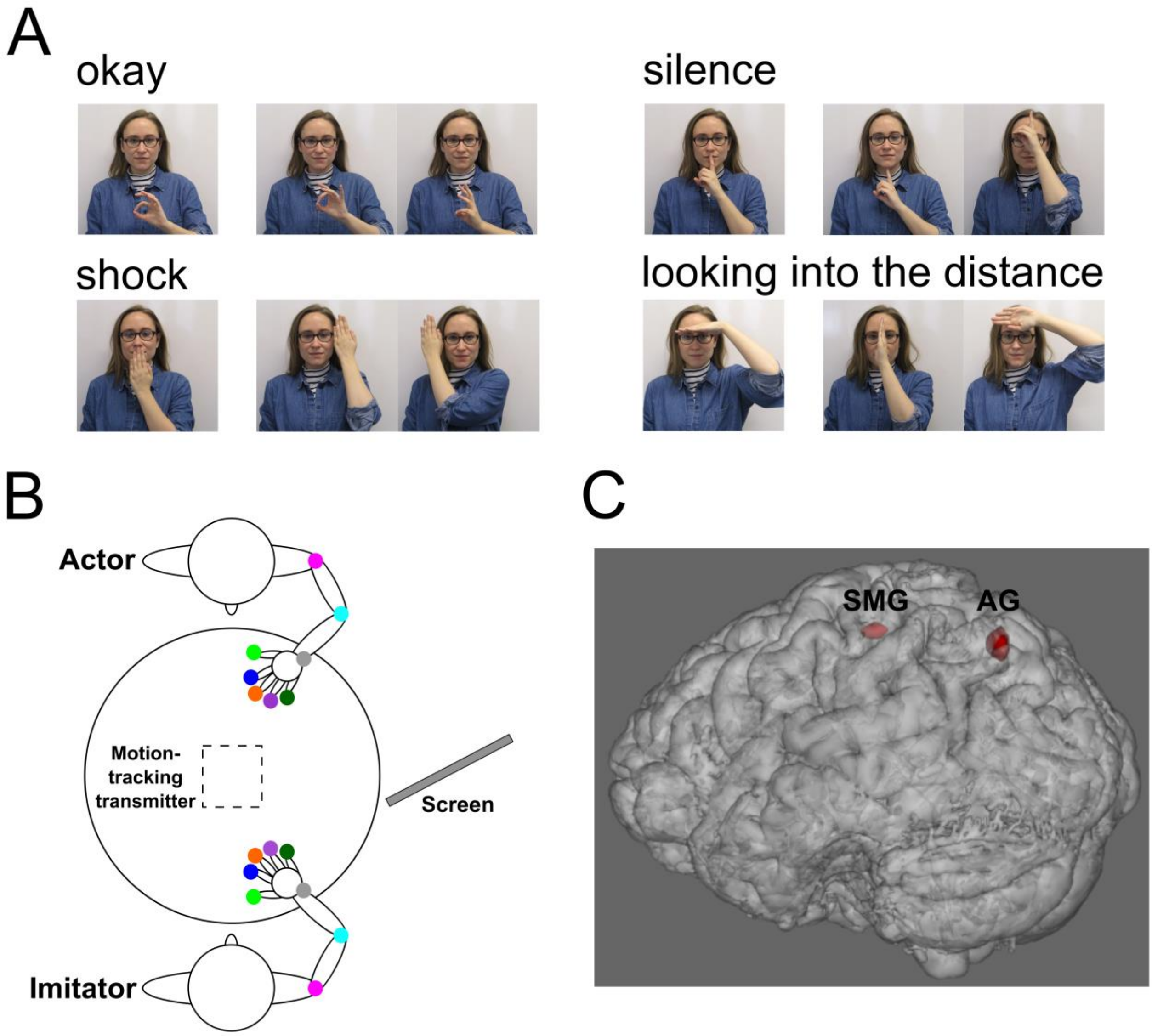

Figure 1: A) Example meaningful finger and hand gestures alongside their matched meaningless counterparts. B) Experimental set-up. Dots indicate the location of motion trackers. The tracking box was placed under the table, and the actor's actions were cued through images displayed on a computer screen that was not observable to the imitator. C) 95% confidence ellipsoids for the TMS target sites shown on a representative participant’s brain. Mean±95% CI MNI coordinates for the SMG: x=-57±2.81 y=-44±4.42 z=44±3.12, and AG: x=-37±4.37 y=-77±3.10 z=40±6.64

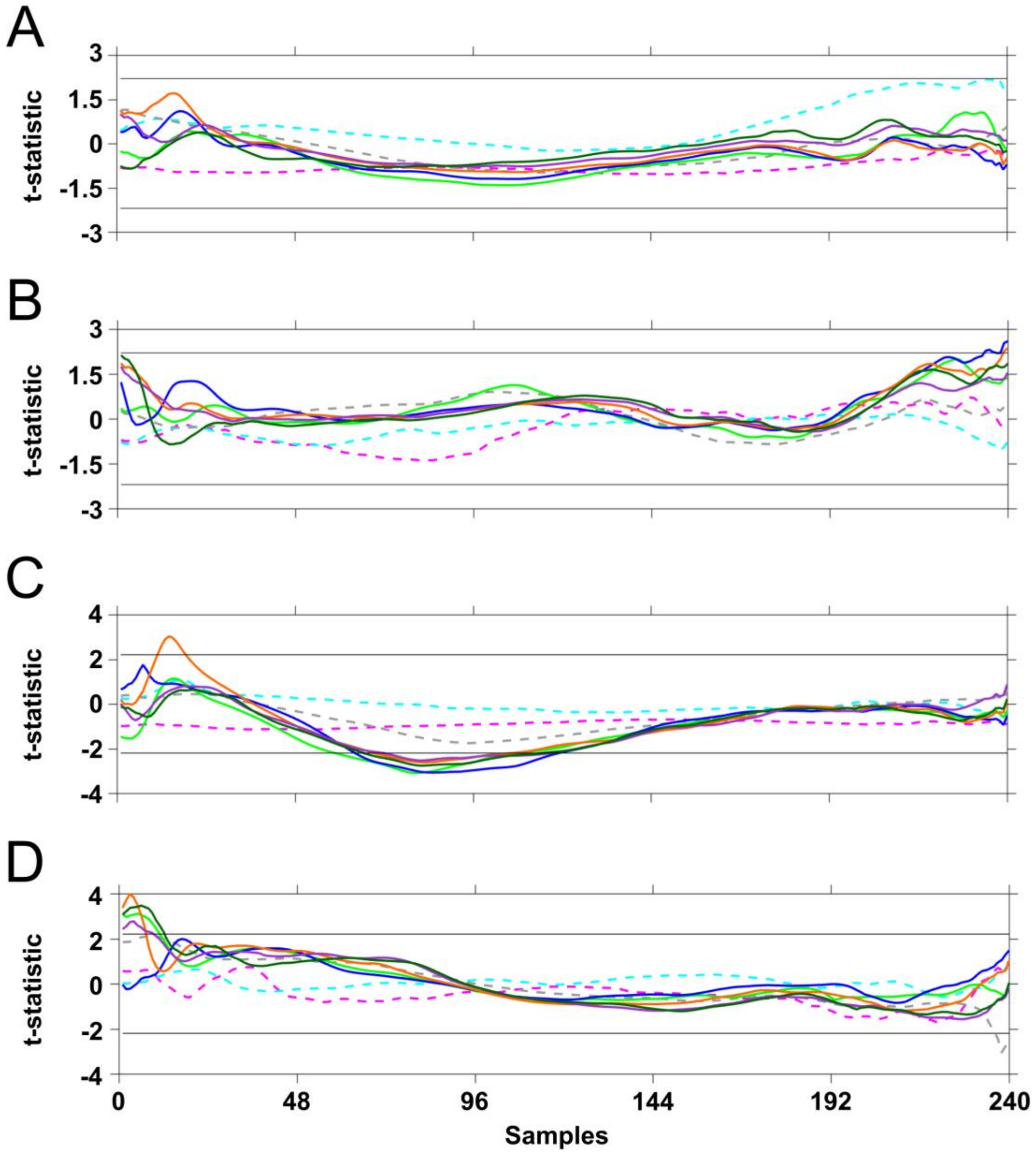

Figure 2: ***t*-statistic plots for resampled comparisons in all trackers; A) SMG versus AG in hand gestures B) stimulation site* meaning interaction in hand gestures C) SMG versus AG in finger gestures D) site*meaning interaction in finger gestures; In all plots the black horizontal lines indicate positive and negative critical *t*-values. Shoulder in dashed magenta, elbow in dashed cyan, wrist in dashed grey, thumb in solid light green, index finger in solid blue, middle finger in solid orange, ring finger in solid purple, little finger in solid dark green (in colour online).**

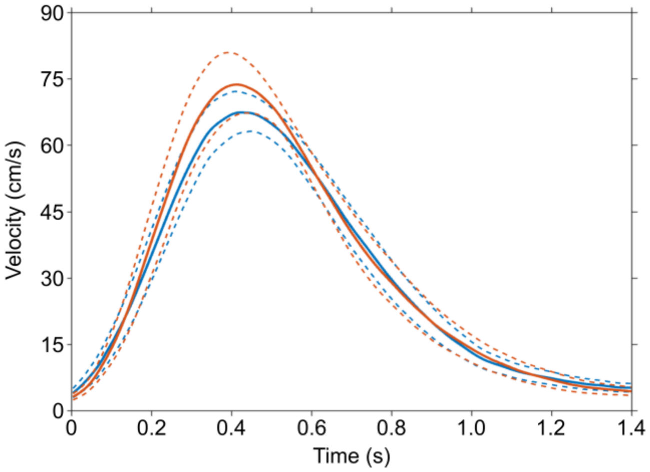

Figure 3: Original mean velocity curve for the thumb comparing SMG and AG in finger gestures. SMG in blue, AG in red (in colour online), dashed lines indicate SE.

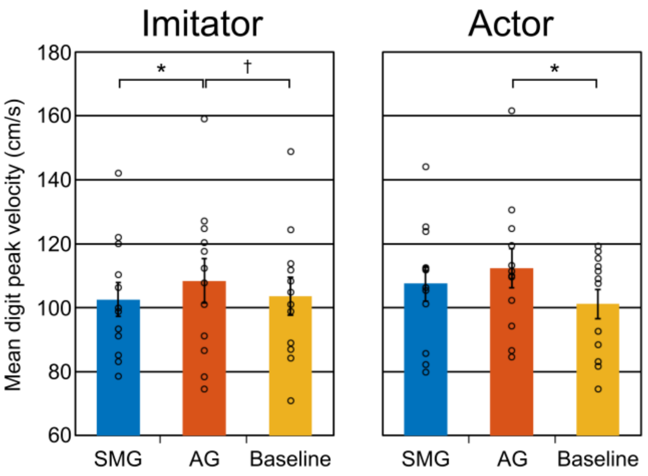

Figure 4: Mean digit peak velocity for finger gestures in imitator and actor data; Error bars indicate standard error, whilst single points show individual participant values. * = *p*<.05 corrected, † = *p*<.05 uncorrected.

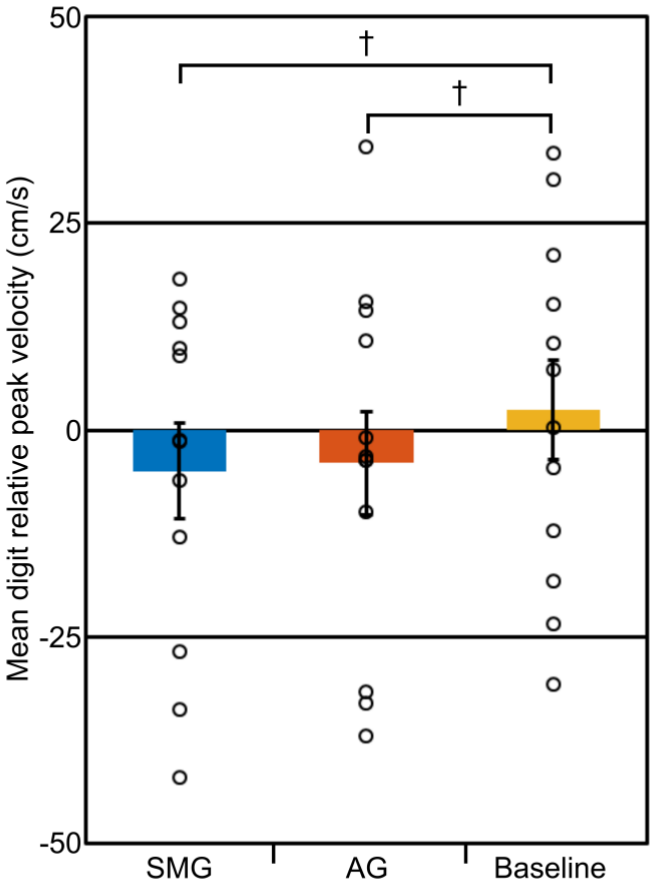

Figure 5: Mean digit peak velocity for finger gestures in imitator relative to actor data; Error bars indicate standard error, whilst single points show individual participant values. † = *p*<.05 uncorrected.