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Intentionally not imitating: Insula cortex engaged for top-down control of action mirroring

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ABSTRACT

Perception and action are inextricably linked, down to the level of single cells which have both visual and motor response properties – dubbed ‘mirror neurons’. The mirror neuron system is generally associated with direct-matching or resonance between observed and executed actions (and goals). Yet in everyday interactions responding to another’s movements with matching actions (or goals) is not always appropriate. Here we examine processes associated with intentionally not imitating, as separable from merely detecting an observed action as mismatching one’s own. Using fMRI, we test how matched and mismatched stimulus-response mapping for actions is modulated depending on task-relevance. Participants were either cued to intentionally copy or oppose a presented action (intentional imitation or counter-imitation), or cued to perform a predefined action regardless of the presented action (incidental imitation or counter-imitation). We found distinct cortical networks underlying imitation compared to counter-imitation, involving areas typically associated with an action observation network and widespread occipital activation. Intentionally counter-imitating particularly involved frontal-parietal networks, including the insula and cingulate cortices. This task-dependent recruitment of frontal networks for the intentional selection of opposing responses supports previous evidence for the preparatory suppression of imitative responses. Sensorimotor mirroring is modulated via control processes, which complex human interactions often require.

KEY WORDS:

Mirror neuron system; action observation; action execution; motor planning; cognitive control; response selection; response inhibition; top-down modulation; Insula Cortex; Supplementary Motor Area; Inferior Parietal Lobule; Mid-Cingulate Cortex; Inferior Frontal Gyrus.

1. INTRODUCTION

The interwoven processes of perception and action form the basis of a person's every experience of, and interaction with, the world. The interactions humans have with each other are particularly important instances of perception and action coupling. The integration of perception-action processes is now thought to occur down to the level of individual neurons that respond similarly when performing and observing a particular action (de Pellegrino et al. 1992; Gallese et al. 1996; for macaque mirror neuron review: Casile, 2013). Since this seminal study, a wealth of literature has addressed the putative functions of the human mirror neuron system (reviewed by Oztop, Kawato & Arbib, 2013), extending beyond actions to emotions, pain and empathy (Keysers & Gazzola, 2009). Regarding sensorimotor mirroring or motor resonance, ongoing debate tackles its purported role in action understanding across multiple sensory domains (see for example, Hickok & Sinigaglia, 2013). Mirror neurons have been suggested to serve a primary function in understanding the states, actions and intentions of another agent (Rizzolatti & Fogassi, 2014). Indeed, individual mirror neurons have been shown to respond to consistent goals of actions even when produced by different muscle effectors (Umiltà, Escola, Intskirveli et al. 2008:

macaques using pliers & reverse-pliers to grasp objects). This suggests that mirror neurons code movement goals for understanding action intentions (Sinigaglia, 2013). Another key function of motor resonance postulated by much of the previous research, is matching sensory representations of others' actions to one's own motor representations. Such mirror-matching is thought to underlie so-called "automatic imitation" (Heyes, 2011). The involvement of the mirror system in overt imitation is itself a subject of interest (see, Brass & Heyes, 2005). However, given the social and communicative nature of humans, it has been argued that motor resonance can emerge through associative learning of related sensory and motoric representations of actions starting in early life. For example, via the repetition of imitative responses between infant and care-giver (Heyes, 2010; Catmur, Walsh & Heyes, 2009; for related Hebbian perspective: Keysers & Gazzola, 2014). So-called mirror neurons and the "mirroring" response are hence typically defined with emphasis on the congruency between observed and executed actions or goals. However, our everyday intended actions are most often not directly mirroring the actions or goals of others around us. So-called mirror neurons and the "mirroring" response are hence typically defined with emphasis on the strict sensorimotor congruency of observed and executed actions, as supported by evidence of automatic imitation. However, our everyday intended actions are most often not directly mirroring the actions of others around us. We therefore propose that more automatic visuomotor 'mirroring' may be controlled task-dependently, to optimally facilitate or suppress tendencies to imitate depending on demands of our current situation or goals.

Automatic imitation refers to the automatic tendency for our own actions to subtly mimic some characteristics of other's actions and can be observed in a variety of paradigms. It has been measured qualitatively as incidents of social mimicry (e.g. Hogeveen, et al. 2014), highlighting the significance of this tendency for non-verbal communication. For intentional movements, another's actions can alter the trajectory of one's own movement. For example, repetitively moving your arm vertically up-down while observing a partner moving their arm horizontally left-right tends to cause a subtly curving motion in your own movements toward aligning with the partner's action (Kilner, Paulignan & Blakemore, 2003). This sensorimotor mapping can also be observed in

reaction time studies, similar to classic stimulus-response compatibility paradigms (Prinz, 1997; Zwickel & Prinz, 2012). Participants display a response time benefit when observing an irrelevant but congruent action stimulus, i.e. a Stimulus-Response Compatibility (SRC) effect for matching actions. This implies that at some level observing an action automatically facilitates imitative responses (Heyes, 2011), and conversely the observation of a mismatching action causes motor interference and a slowing of reaction time (Kilner, et al., 2003; Brass et al. 2000; Brass, Derrguss & Von Cramon, 2005).

In real-world settings, the relationship between our own movements and the actions of those with whom we interact are varied and changeable. The tendency towards imitative responses is not always appropriate for our own actions. It is often necessary to perceive someone's action while concurrently preparing a difference movement oneself. For instance, in partnered dancing, performing a spin in response to one's partner stepping back and lifting their arm. Several studies have related activity in putative human mirror system regions to related but dissimilar stimulus-response pairs, such as during the preparation of complementary actions (Newman-Norlund et al., 2007; Newman-Norlund et al., 2008; Ocampo et al., 2011). A growing body of work has begun to examine the relationship between automatic imitation and task goals for matching or non-matching actions (Bien, Roebroek, Goebel & Sack, 2009; Brass, Ruby & Spengler, 2009; Bardi, Bundt, Notebaert & Brass, 2015; Cross et al., 2013; Cross & Iacoboni, 2014b; 2014a). Such work suggests that mirroring is open to preparatory and reactive control mechanisms. Together these lines of enquiry highlight that the perception-action coupling of mirror responses is not only a matter of simple direct-matching (Oztop, Kawato & Arbib, 2013).

The typical definition of "mirroring" in action places emphasis on the strict sensorimotor congruency of observed and executed actions. Representation of this matching action is reflected in individual neurons that respond similarly when performing and observing a particular action (de Pellegrino et al. 1992; Gallese et al. 1996; for macaque mirror neuron review: Casile, 2013). Given the complexity of social interactions, it is logical that mirroring would be modulated

depending on task-set, involving processes associated with higher-order executive functions, or cognitive control, which enable one to coordinate behaviour toward meeting internal goals, while remaining flexible to changing demands (Botvinick et al., 2001; Dosenbach et al., 2008; Koechlin et al., 2003; Miller & Cohen, 2003; Ridderinkhof et al., 2004). Cognitive control processes are underpinned by a large number of regions which are organised into two dissociable networks: a 'cingulo-opercular' network for stable goal maintenance (i.e. *proactive control*), and a 'fronto-parietal' network for initiating and adjusting control moment-to-moment (i.e. *reactive control*). How cognitive control processes intersect automatic visuo-motor mapping is unclear (for a detailed review see Campbell & Cunnington, 2017).

A series of studies by Cross and colleagues (Cross et al. 2013; Cross & Iacoboni, 2014a, 2014b) have framed the modulation of stimulus-response mapping within a dual-route model (Braver, 2012). An *automatic* fast route links learned stimulus-compatible responses and a second parallel, but *intentional and indirect*, route links stimulus and response according to current task demands. Counter-imitation requires this automatic-route to be suppressed while the slower task-relative intentional-route enables the stimulus-incompatible response. Using fMRI to investigate this model, Cross and Iacoboni (2014a) related preparatory suppression (that is, the intentional indirect route) to cortical areas including left dorso-lateral pre-frontal cortex, frontal pole, posterior parietal cortex, and early visual regions. This extends on an earlier study in which the control of imitation additionally involved the anterior cingulate, anterior insula and frontal operculum (Cross et al. 2013). Transcranial magnetic stimulation (TMS) evidence has further supported this model to show imitation-compatible motor excitability was suppressed, relative to baseline, when participants were intentionally preparing to counter-imitate or when the stimulus-response mapping was unknown (no-preparation trials; Cross & Iacoboni, 2014b). Hence, the tendency for automatic activation of stimulus-compatible responses can be strategically suppressed when this would interfere with task demands. The authors surmise that this occurs via top-down modulation of mirror system activity. Our current fMRI study addressed this question by directly manipulating both the task-relevance of action observation to performed actions, as

well as compatibility of observed and performed actions. We did this by pre-cuing participants to either intentionally copy or oppose a presented action or to perform a pre-specified action that incidentally matched or mismatched the presented action. Work-to-date has yet to address whether the interference to one's own actions from the incidental observation of mismatching actions is separable from a modulation of mirroring processes when one must intentionally perform opposing or mismatching actions as necessary for task-goals. Our current experiment directly addressed this issue.

1.1 CURRENT STUDY

Our paradigm manipulated both the congruency of observed and executed actions (matched versus mismatched) and the task relevance of observed actions to executed actions (either incidental or intentional), in a two-by-two factorial design. Figure 1 depicts the combinations of task cues for action preparation and visual stimuli. Through this manipulation of task-relevance we aimed to compare proactive and reactive control of automatic imitation (contrast of intentional and incidental mismatching or counter-imitation), and dissociate the neural networks of each. Importantly, the current paradigm employed intransitive and directly opposing actions that were mutually exclusive. In this sense, the motor plans for the two actions have little overlap and should be clearly dissociable. Previous paradigms have often relied on opposing effectors to manipulate imitative compatibility. Much work has employed the paradigm of Brass et al. (2000) with movements made using different fingers on the same hand. These actions could conceivably be incorporated into a single motor plan (moving both fingers) and somewhat confound the manipulation of stimulus-compatibility. Our pair of opposing actions cannot physically be performed at the same time (opening and closing the right hand; see figure 1 images showing final position of hand actions) and are differentiated by flexor and tensor hand muscle activity. This creates greater conflict between the two motor plans.

As previous work on imitation and action 'mirroring' would suggest, we expected our action observation-execution task to highlight putative human mirror system regions. Meta-analyses have implicated the inferior frontal gyrus (IFG), ventral and dorsal premotor cortex

(PMv, PMd) and, superior and inferior parietal lobule (SPL, IPL, and superior temporal sulcus (STS) as mirror network areas (Molenberghs, et al., 2012). Where imitation is explicitly task-relevant (intentional imitation), it is plausible that activation within mirror areas will be greater than when responses are not intentionally imitative (i.e. for incidental conditions or intentional mismatching actions). This would imply an interaction effect between task-relevance and congruence, such that activation in mirror region areas may be greater specifically for intentional imitation compared with all other conditions. Regarding overall effects of congruency, or matching versus mismatching between observed and executed movements, we would expect greater activation in areas typically associated with response conflict or stimulus-response incompatibility for mismatching actions, including the anterior cingulate, insula cortex and frontal operculum and dorsolateral prefrontal cortex (Dosenbach et al., 2008). Of particular interest, however, is how activation for mismatching actions may change depending on the task-relevance, when participants must intentionally oppose the observed action compared with performing a pre-specified action that incidentally mismatches the observed action. For intentional mismatching (i.e. when pre-cued to counter-imitate by performing the opposing action to that observed), we may expect to see greater recruitment of cognitive control processes for top-down regulation of more automatic mirroring processes. This would further support the findings of Cross and Iacoboni (2014b) and may optimally allow suppression of processes underlying automatic imitation and facilitate the selection and performance of appropriate opposing actions.

2. METHODOLOGY

2.1. PARTICIPANTS

Twenty-four healthy, right-handed (Handedness Inventory, Oldfield, 1971), volunteers were recruited via the University of Queensland Psychology Research Participation Pool (13 females; mean age = 23.5, SD=3.3). Participants gave their informed consent and were offered monetary compensation for their time commensurate with transport costs, in accord with ethics

requirements. The Medical Research Ethics Committee of the University of Queensland approved the study.

2.2. BEHAVIOURAL PARADIGM

Participants observed and performed simple hand opening and hand closing actions while in the MRI scanner. These were intransitive actions made with the right hand, starting from a neutral position palm-down and fingers extended and in line with the wrist resting on an ergonomic cushioned support. Keeping the wrist in contact with the support, the open-hand action required the palm to be raised with fingers spread apart, then returning to the neutral position. The close-hand action started by bringing all five digits together in a precision grip, while maintaining wrist position and then return to neutral (see figure 1, example frames from videos of action-stimuli demonstrate end position of responses). Thus, these actions were directly opposing in terms of the engagement of flexion and tension muscles of the right hand. Unlike previous ‘counter-imitation’ paradigms (e.g. index and little finger extensions) the actions employed here were mutually exclusive – one cannot open and close the same hand at the same time.

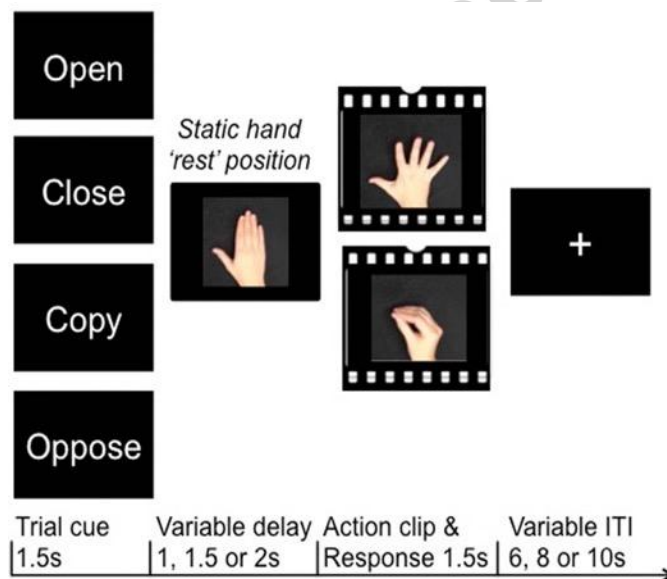


Figure 1. Schematic representation of an experimental trial and all possible conditions (cue-stimulus combinations). This paradigm fit a 2x2 factorial manipulation of stimulus-response

compatibility (matched/mismatched) and preparation context (intentional/incidental) to target both intentional and incidental imitation and counter-imitation. Note: not to scale of presentation.

The task involved concurrent action execution and action observation, with the observed action being a video clip of a hand opening or closing that was either congruent or incongruent to the action performed by the participant. Crucially, there were two preparation contexts depending on the stimulus-response relationship:

- 1) Incidental: Participants were cued to perform a specific action, either hand opening (“Open”) or hand closing (“Close”), independent of the observed action. The following observed action video could either be congruent or incongruent with the pre-defined action performed by the participant, giving rise to conditions of *incidental imitation* and *incidental counter-imitation* responses.
- 2) Intentional: Participants were cued to perform an action dependent on the action observed in the video clip, either imitating the action observed (“Copy”) or counter-imitating the action observed (“Oppose”). This gave rise to conditions of *intentional imitation* and *intentional counter-imitation*. Stimulus presentation and timing was controlled with a custom Psychtoolbox program run in MATLAB2014 (Brainard, 1997; Pelli, 1997).

For all conditions, participants were instructed to perform the cued action as quickly and accurately as possible upon seeing the on-screen hand commence movement. As such the imperative cue to move was always the action-onset in the video clip, even on trials when the response action was predefined. To ensure that participants could not anticipate the time of movement onset and responded appropriately to the action onset in the video clip, the onset time was varied pseudo-randomly between trials by extending the duration of the first static frame depicting a ‘rest’ position hand (1, 1.5 or 2s delay, followed by 1.5s action clip). Lastly, a fixation cross was displayed between trials for a variable inter-trial interval (ITI) of 6, 8 or 10s. The variable ITI and stimulus-onset delay were employed to optimize the event-related fMRI design

by jittering the timing of events across the image acquisition sequence to maximise estimation efficiency (Huettel et al., 2009). Moreover, these periods of fixation served as the implicit baseline for the fMRI analysis.

The order of conditions was randomized within each run with trial durations between 9.5 and 14s (action cue: 1s; variable delay: 1, 1.5 or 2s; action clip: 1.5s; variable ITI: 6, 8 or 10s). One fMRI run consisted of 48 trials, 12 of each of the 4 conditions (with equal numbers of hand-open and hand-close videos presented within conditions), for a total duration of approximately 11 minutes. The paradigm was repeated for 4 fMRI runs.

The four conditions formed a 2x2 factorial design with Congruence (match versus mismatch) and Preparation Context (intentional versus incidental) as factors. The task was not designed to be challenging so that few errors would be expected; participants simply had to perform open or close actions as indicated by the cues. High accuracy rates for this task were confirmed during pilot-testing in a sample of eight participants (6 females) with mean age 23.4 years (SD 2.9 years), mean percentage correct for each condition: incidental imitation 92% (SEM 4%), incidental counter-imitation 92% (SEM 4%), intentional imitation 96% (SEM 3%), intentional counter-imitation 96% (SEM 2%). An ANOVA (2x2 repeated measures) revealed no statistically significant differences, Congruence: $F(1,7)=0.496$, $p=.504$, $\eta^2 = 0.066$; preparation context: $F=4.091$, $p=.083$, $\eta^2 = 0.369$; interaction: $F(1,7)=0.247$, $p=0.634$, $\eta^2 = 0.034$.

2.2.1. STIMULI

Stimuli were recorded on a SONY Digital Video Recorder (HDR-XR150E 'Handycam'; 25 frames per second, Dimensions 720x576, bitrate 30,336), and edited using Adobe Premier Pro CS6 on OSX. Two actors (one male, one female) performed the open/close hand actions against a black backdrop with the hand centred within frame. Videos of each actor performing each action were edited to provide three different action onsets. For each actor, a single still image of the neutral starting position was used as the first frame for videos of both actions. This frame was

prolonged for three durations (1, 1.5 or 2 seconds), providing a variable delay before the movement stimulus onset. The variable delay ensured that participants could not predict action onset in the video and respond pre-emptively. Following this variable duration still frame of neutral hand position, the “open” or “close” hand action frames played for a duration of 1.5 s, matched across all clips (digital footage edited in Adobe Premier Pro version 11.1.0 on OSX). This produced 12 different action video-clips (2 actors x 2 actions x 3 delay periods).

2.2.2. RESPONSE RECORDING WITH MOTION CAPTURE

Responses were recorded using a Qualisys Motion Capture system, including two wall-mounted cameras, controlled by the Qualisys Track Manager software run on a PC within the 3T scanner operator console. Two markers attached to the tips of participants’ thumb and index finger captured movement trajectories during the behavioural paradigm to distinguish the two actions and measure action onsets for reaction-time data. Motion capture (at 250 frames per second) was triggered 200ms before stimulus presentation and reaction time was measured as response-onset relative to observed action-onset. To identify response onset time from the motion capture data, the trajectory data from the index and thumb marker positions across X, Y and Z planes were analyzed. The moving averages and standard deviations of X, Y, and Z positions across trials were calculated and the movement onset time was defined as the first time-point at which any of these positions crossed above one standard deviation of the moving average (see also Mehrkanon et al., 2014). Accuracy of the behavioural performance was assessed qualitatively, with responses observed by the experimenter during the task and with almost no errors observed. This was expected given: 1) the task was very simple and well understood by participants, having completed several training blocks prior to entering the scanner; and 2) very high accuracy was found for this task in the prior pilot study (>92% correct across all conditions), which had trials displayed at a faster rate.

2.3. MRI ACQUISITION AND PREPROCESSING

Functional and structural imaging was performed using a whole-body 3-Tesla Siemens Trio MRI scanner (Siemens Medical System, Germany) equipped with a 32-channel head coil. Four functional imaging runs of 11 min each and an additional structural image were acquired in a single 1-hour scan session.

Functional images were acquired with a simultaneous multi-slice (multiband) gradient-echo echo-planar imaging (GE-EPI) sequence with the following parameters: 44 axial slices; echo time (TE) 32.0ms; repetition time (TR) 700ms; flip angle (FA) 70°; pixel bandwidth 1698; Field of View (FOV) 200 × 200mm and 74 x 74 voxel matrix; 3.0 x 3.0 x 3.0 mm³ with 10% slice gap, whole brain coverage, with multiband slice acceleration factor 4. For the anatomic image, we employed an MP2RAGE sequence with the following parameters: TE = 2.32ms, TR = 1900ms, FA = 9°, 256 × 256 cubic matrix, voxel size = 0.9 × .09 × 0.9mm³, to acquire high-resolution, whole-brain, T1-weighted structural images for anatomical reference and co-registration of functional images.

Functional data were processed using SPM8 (Wellcome Trust Department of Imaging Neurosci, Institute of Neurology, London, www.fil.ion.ucl.ac.uk/spm) implemented in MATLAB (R2015b, Mathworks). Preprocessing included spatial realignment, co-registration with individual structural images, spatial normalisation, and spatial smoothing. EPI images were first spatially realigned via 6-degree affine transformation to the first image of each scan and between scans for head movement correction. Realigned images were spatially normalised via nonlinear transformation to MNI space via co-registration with the anatomic T1 image and transformation parameters obtained via the segment process in SPM8. Functional images were re-sliced to 2 x 2 x 2 mm³ and spatially smoothed with a 6mm full width at half maximum (FWHM) isotropic Gaussian kernel.

2.4. ANALYSES

2.4.1. BEHAVIOURAL ANALYSIS

Reaction times computed from the motion capture data were compared across conditions with 2x2 within-subjects ANOVA. The motion capture recordings from four participants were unreliable, with missing data from occluded markers resulting in less than a third of trials available for analysis in each condition. Thus, a subset of 20 participants was included in the analysis of behavioural measures.

2.4.2. FMRI ANALYSIS

General linear modelling (GLM) was used to estimate statistical parametric maps of task-related BOLD-signal changes for each of the four conditions. The onset of the action-stimulus movie, being the imperative to perform an action, was used to build response regressors for concurrent action observation and motor execution, modelled as box-car functions of 1s duration convolved with the haemodynamic response function (HRF). Periods of fixation between trials were not explicitly modelled and served as an implicit baseline in the model.

At the first-level of GLM analysis, parameter estimates for each individual participant were obtained for each of the four task conditions (*intentional/incidental match* and *mismatch*), each compared to the implicit baseline (rest). These individual parameter estimates were entered into a second-level group analysis using a 2x2 flexible factorial model, with *Preparation Context* (intentional and incidental) and *Congruence* (match and mismatch) being the factors.

Group-level statistical maps for F- and T-contrasts were overlaid onto a MNI template brain for visualisation (created in MRIcroGL, www.nitrc.org/projects/mricron). Cluster and peak labels were applied by the Automated Atlas Labelling toolbox within SPM8 (Tzourio-Mazoyer et al., 2002). For both F- and T-contrasts at the group level, significant activation was defined by a peak-level threshold of $P(\text{FWE}) < 0.05$ corrected for multiple comparisons, with no further correction based on cluster size.

3. RESULTS AND DISCUSSION

3.1. REACTION TIME EFFECTS

Participants maintained high correct response rates across all conditions, as noted by visual observation during the task, and as expected given that the task was designed not to be difficult. Average reaction times from the motion-capture measures were submitted to a 2x2 within-subjects ANOVA, showing a significant main effect of Congruency, $F_{(1,19)}=5.817$, $p=.026$, *partial* $\eta^2=0.234$, and a significant main effect of Preparation Context, $F_{(1,19)}=19145.855$, $p<0.0001$, *partial* $\eta^2=0.885$, and no significant interaction between these factors, $F_{(1,19)}=0.128$, $p=0.724$, *partial* $\eta^2=0.007$. As can be seen in Figure 2, reaction times were significantly faster overall for matching compared with nonmatching actions, showing a typical reaction time cost for incongruent (mismatching) stimulus-response conditions. Reaction times were also significantly faster for incidental conditions compared with intentional conditions, reflecting a reaction time cost when the action to perform could only be selected after evaluating the observed action (to copy or oppose in the intentional condition) compared with performing a predefined action (to open or close in the incidental condition).

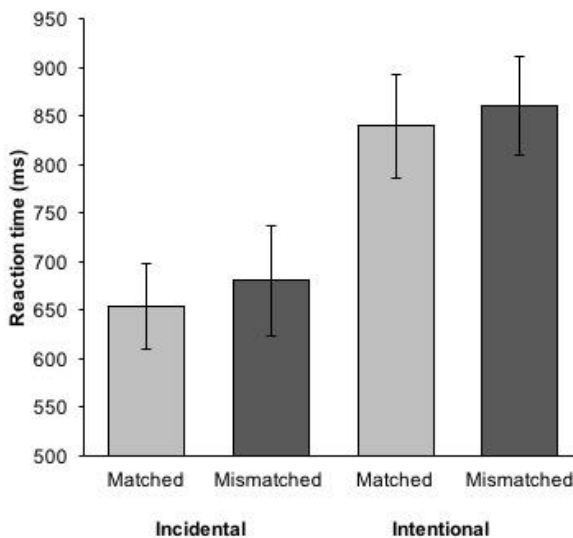


Figure 2. Reaction times for *matched* and *mismatched* congruency between observed and executed actions, for contexts in which the pairing was *incidental* (performing predefined open or close actions) compared with *intentional* (copying or opposing the observed action). Error bars show 95% confidence intervals.

3.2. FUNCTIONAL IMAGING RESULTS

The critical feature of our paradigm was the separation of intentional from incidental congruency between observed and executed actions by manipulating the task-relevance of observed actions. We considered conditions in which the observed action was explicitly task-relevant (cued to ‘copy’ or ‘oppose’) as *intentional* imitation or counter-imitation. Thus, we could examine task-dependent control of ‘mirroring’ processes depending on the task-relevance of the observed actions.

As a first-step, a 2x2 within-participants ANOVA was conducted using a flexible factorial analysis with factors of Preparation Context (intentional, incidental) and Congruence (match, mismatch). F-contrasts were used to identify brain regions showing significant main effects of Congruence, Preparation Context, or interactions between these factors (Figure 3; Tables 1-3). Note that these F-contrasts are two-tailed, hence they show all areas that had significant effects independent of the direction of differences between conditions. Subsequent T-contrasts (below) show more specifically where activation was greater for mismatching versus matching actions, and vice-versa, and for intentional versus incidental mismatching actions.

As can be seen in Figure 3, main effects of Congruency, showing differences overall between matching and mismatching stimuli, were found predominantly in frontal regions including the insula and cingulate cortices and the inferior frontal gyrus (green clusters). Main effects of Preparation context, showing differences between intentional and incidental conditions, were centred in the SMA and the left middle occipital gyrus (yellow clusters).

A significant two-way interaction between Preparation Context and Congruence was found in two peaks within the middle occipital cortex, bordering on the inferior parietal lobule. Although these individual peaks met our strict statistical threshold of peak-level $p(\text{FWE-corrected}) < 0.05$, they were isolated voxels rather than clusters of activation. At a more lenient voxel-level probability of $p(\text{uncorrected}) < 0.0001$, these peaks formed a single cluster of 120 voxels,

significant with cluster-size probability of $p(\text{FWE-corrected}) < 0.05$, that extended into the angular gyrus of the inferior parietal lobule (Figure 3, purple cluster, presented at peak-level $p(\text{uncorrected}) < 0.0001$ and cluster-level $p(\text{FWE-corrected}) < 0.05$ for display purposes).

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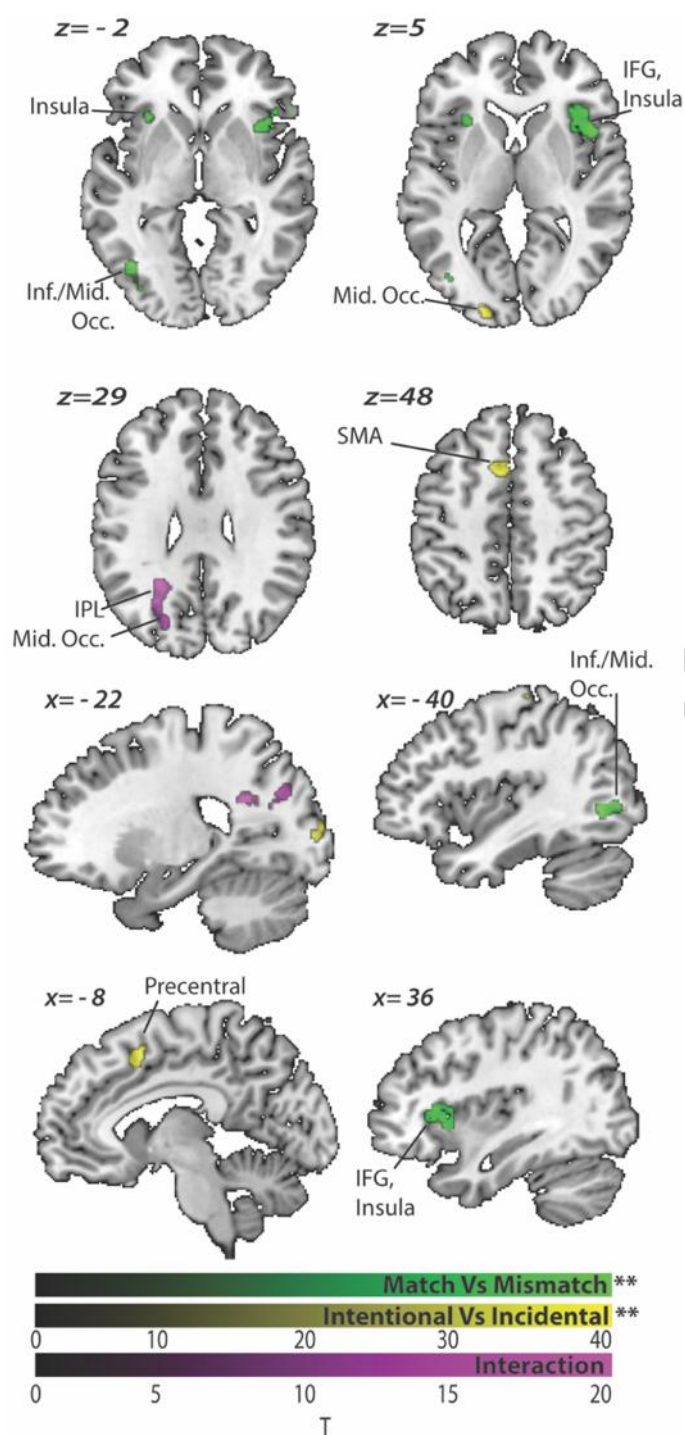


Figure 3. Brain areas showing significant main effects of Congruence (match versus mismatch; Green clusters), main effects of Preparation Context (intentional versus incidental; Yellow clusters), and

significant interaction effects (Purple clusters). Main effects displayed at peak-level ** $p(\text{FWE}) < 0.05$ and interaction effect at peak-level $p(\text{uncorrected}) < 0.0001$ and cluster-level $p(\text{FWE}) < 0.05$. Statistical parametric maps are overlaid on axial (MNI z coordinates indicate slice-depth) and sagittal brain slices (MNI x coordinates indicate lateral slice-position). Colour bars are displayed for each, with height-threshold T indicated. Anatomical Abbreviations: IFG: Inferior Frontal Gyrus; IPL: Inferior Parietal Lobule; Inf./Mid. Occ.: Inferior & Mid Occipital Gyri.

Parameter estimates, representing the level of activation across the four conditions, were extracted for the peak voxel showing this significant interaction effect (co-ordinates: -28, -66, 26 in the mid-occipital; Figure 4). As can be seen in Figure 4, the significant interaction was related to greater activation specifically for the intentional matching condition compared with all other conditions. Thus, the condition in which the participant was pre-cued to intentionally copy, or mirror, the observed action was associated with greater activation in the mid-occipital and inferior parietal region.

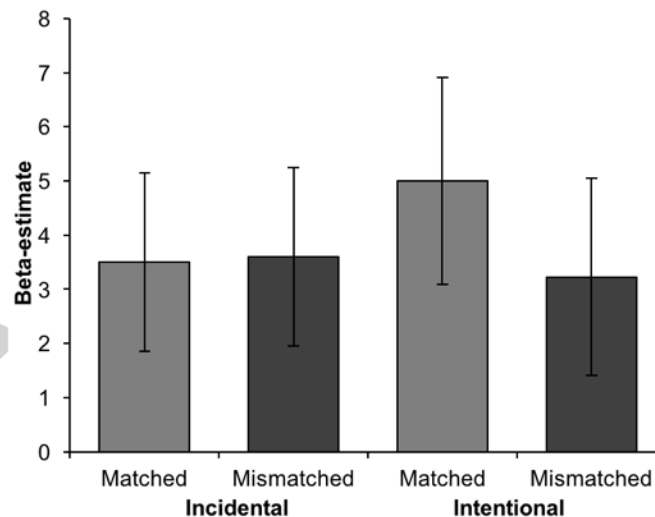


Figure 4. Parameter estimates, representing level of activation, for the peak voxel (coordinates: -28, -66, 26) within the mid-occipital (bordering the inferior parietal) region that showed a significant interaction effect between Preparation Context (incidental, intentional) and Congruence (Matched, Mismatched). Error bars show 95% confidence intervals around the mean.

Table 1. Main effect of stimulus-response Match versus Mismatch

Cluster				Peak Statistics			
label	% labeled	k	x,y,z {mm}	label	p(FWE)	F	Z
Putamen	52.8	771	36 16 0	Insula	<0.001	68.7	6.78
IFG Tri	20.8		38 26 4	Insula	<0.001	61.69	6.51
IFG Orb	12.3		44 12 6	IFG Oper	<0.001	59.86	6.44
IFG Oper	9.6						
Inf Occ	83.2	273	-42 -70 -2	Mid Occ	<0.001	64.76	6.63
			-38 -82 0	Mid Occ	<0.001	46.58	5.83
			-36 -88 8	Mid Occ	0.001	42.35	5.61
IFG Oper	7.6	289	-30 20 2	Insula	<0.001	54.31	6.2
Insula	4.8		-30 20 -8	Insula	0.001	44.75	5.74
			-44 14 0	Insula	0.001	43.11	5.65
SupraMarg. (IPL)	1.2	83	64 -40 36	SupraMarg. (IPL)	<0.001	53.02	6.14
SMA	50.8	130	12 10 68	SMA	<0.001	50.64	6.03
			20 0 62	Sup Frontal	0.002	39.94	5.47
			14 0 72	Sup Frontal	0.006	36.29	5.26
Sup MFG	54.2	107	10 18 38	MCC	<0.001	48.1	5.91
			4 10 54	SMA	0.004	37.86	5.35
			10 18 56	SupraMarg. (IPL)	0.006	36.57	5.27
Fusiform	50	10	-30 -40 -12	Fusifrom	0.004	37.99	5.36
Parahippo.	10						
SupraMarg. (IPL)	28.6	7	-62 -48 34	SupraMarg. (IPL)	0.009	35.21	5.19
IPL	14.3						
Sup Temp	61.5	13	62 -38 24	Angular (IPL)	0.017	33.02	5.05
Angular (IPL)	20	5	-44 -68 36	Angular (IPL)	0.02	32.53	5.01
Precuneus	20	5	-2 -56 24	Precuneus	0.027	31.51	4.94
ACC	100	1	6 18 26	ACC	0.031	31.05	4.91
Precentral	100	1	38 4 48	Precentral	0.039	30.24	4.85
Mid Temp	100	1	54 -32 -2	Mid Temp	0.043	29.96	4.83
unlabeled	100	1	-28 8 18	Insula	0.049	29.49	4.8

Notes: labelling via Automatic Anatomic Labelling (AAL) toolbox. Abbreviations: IFG: Inferior Frontal Gyrus; IFG Tri.: IFG pars triangularis; IFG Orb.: IFG pars orbitalis; IFG Oper.: IFG pars opercularis; IPL: Inferior Parietal Lobule; Supramarg.: Supramarginal gyrus.

Table 2. Main effect of Intentional versus Incidental action preparation

Cluster				Peak Statistics			
labels	% labeled	k	x,y,z {mm}	label	p(FWE)	F	Z
Sup MFG	89.1	174	-4 14 48	SNA	0	84.19	7.3
SMA	4.6						
Sup Frontal	2.3						
Mid Occ	8.6	175	-20 -94 4	Mid Occ	0	52.55	6.12
Postcentral	64.6	48	-42 -26 64	Postcentral	0	47.29	5.87
Insula	11.11	18	32 18 6	Insula	0.002	40	5.48
Mid Frontal	25.8	31	-30 -2 48	Precentral	0.004	38.31	5.38
Precentral	3.2		-24 2 54	Mid Frontal	0.035	30.61	4.88
MCC	82.6	23	10 12 46	SMA	0.004	37.47	5.33
SMA	4.4						
Insula	5.2	19	-30 22 4	Insula	0.006	36.48	5.27
Mid Occ	4.5	22	32 -92 6	Mid Occ	0.007	36.05	5.24
Mid Occ	3.7	27	-32 -90 4	Mid Occ	0.009	35.18	5.19
Mid Frontal	11.11	9	-36 20 42	Mid Frontal	0.011	34.56	5.15
MCC	16.67	6	6 26 32	MCC	0.017	32.99	5.04
IPL	33.33	3	-30 -50 48	IPL	0.017	32.93	5.04
Precuneus	100	1	10 -54 40	Precuneus	0.027	31.49	4.94
MCC	20	5	8 20 38	MCC	0.029	31.21	4.92
Angular (IPL)	50	2	-42 -72 40	Angular (IPL)	0.031	31.01	4.91
Calcarine	100	1	-22 -62 8	Calcarine	0.035	30.6	4.88
ACC	25	8	-6 24 30	ACC	0.036	30.51	4.87
Precentral	100	1	-34 -16 64	Precentral	0.041	30.08	4.84
Postcentral	100	1	-36 -28 56	Postcentral	0.046	29.69	4.82
Angular (IPL)	100	1	-44 -68 36	Angular (IPL)	0.047	29.62	4.81
Angular (IPL)	50	2	46 -72 36	Angular (IPL)	0.049	29.52	4.8

Notes: labelling via Automatic Anatomic Labelling (AAL) toolbox. Abbreviations: ACC: Anterior Cingulate Cortex;

IPL: Inferior Parietal Lobule;; Sup MFG: Superior Medial Frontal Gyrus; Sup.: Mid Occ.: Mid Occipital Gyrus; MCC: Middle Cingulate Cortex; SMA: Supplementary Motor Area; Supramarg.: Supramarginal gyrus.

Table 3. Interaction between Congruence and Preparation Context

Cluster labels	% labeled	k	x,y,z {mm}	Peak Statistics			
				label	p(FWE)	F	Z
Mid Occipital	100	1	-28 -66 26	Mid Occipital	0.014	33.53	5.08
Mid Occipital	100	2	-24 -54 28	Mid Occipital	0.021	32.29	5.00

NOTES: CLUSTER AND MAXIMA LABELS VIA AUTOMATIC ANATOMIC LABELLING (AAL) TOOLBOX.

3.2.1. CONGRUENCY BETWEEN OBSERVED AND EXECUTED ACTIONS

Regarding effects of congruency, the F-contrasts above showed a predominantly frontal network, including bilateral insula cortex and inferior frontal gyrus, that showed significant differences in activation for matching compared with mismatching between observed and executed movements (Figure 3; Green clusters). To examine these effects more specifically, we conducted T-contrasts to compare activation for matched versus mismatched actions, and vice-versa, separately for intentional conditions (“copy” versus “oppose”) and for incidental conditions (Figure 5; Tables 4-6). Although all of these contrasts represent effects of congruence or stimulus-response compatibility, the intentional and incidental conditions distinguish between pro-active and reactive control (Braver, 2012). For intentional conditions (with cues to “oppose” or “copy”) preparatory suppression or facilitation of mirroring could be engaged, while for incidental conditions (performing pre-defined “open” or “close” actions) only reactive control could be involved.

As can be seen in Figure 5, the congruency effects in the bilateral insula and cingulate cortices and the inferior frontal gyrus were associated with greater activation for mismatching actions than for matching actions, particularly for the intentional condition (red colours). This pattern of BOLD-signal changes supports our hypothesis that frontal control networks are integrated with action observation processes during counter-imitation. Moreover pointing to possible neural substrates for the process of overcoming motor interferences from the tendency toward imitating observed actions (Brass, et al. 2000, 2005; Kilner et al. 2003), given such processes would be common to both mismatch conditions.

Congruency effects in more posterior areas, particularly the left mid occipital and inferior parietal regions, were associated with greater activation for matching actions than for mismatching actions, again particularly for the intentional condition (dark blue colours). Note that for incidental conditions, there were no areas showing significantly greater activation for matching compared with mismatching actions at our strict statistical threshold (peak-level $p(\text{FWE}) < 0.05$). For display (Figure 5, light blue) and in Table 6 we have shown areas defined by a more lenient peak-level threshold $p(\text{uncorrected}) < 0.001$, with cluster-level probability $p(\text{FWE}) < 0.05$ corrected for multiple comparisons. Those subthreshold areas included a cluster within the left precuneus and posterior cingulate cortex (153 voxels; peak at -2, -56, 22; $T = 4.90$) and a smaller cluster in the mid occipital cortex (131 voxels; peak at -36, -84, 0; $T = 4.50$).

For intentional conditions, greater activation was found for matching compared with mismatching actions in two main posterior regions (Figure 5, dark blue; Table 4). The first region was more inferior in the mid occipital gyrus, overlapping with the subthreshold area reported above for the same contrast in incidental conditions (499 voxels; peak at -42, -70, -2; $T = 7.07$). This is also the same area that showed a main effect of Congruency in the F-contrast analysis (Figure 3, yellow cluster), suggesting overall greater visual activation when participants made imitative responses, whether incidentally or intentionally. The second region was more superior in the mid occipital gyrus bordering on the inferior parietal lobule (52 voxels; peak at -30, -88, 22; $T = 6.03$; and 12 voxels; peak at -28, -66, 26; $T = 5.94$), overlapping with the region showing the significant interaction effect in the F-contrast analysis (Figure 3, purple cluster, and parameter estimates plotted in Figure 4). This region showed significantly greater activation for imitative compared with non-imitative actions specifically for the intentional condition (as shown by the significant interaction effect and the plot of parameter estimates), reflecting greater recruitment of this action observation area specifically when participants were pre-cued to intentionally imitate the observed action.

3.2.2. INTENTIONAL COUNTER-IMITATION

The significant activation for mismatching compared with matching actions (Figure 5, red and orange overlays) showed only restricted areas of overlap in the right insula and inferior frontal gyrus; however, intentional counter-imitation also recruited the left insula, with these bilateral insula clusters being much more widespread than for incidental conditions (see tables 5 and 7 for cluster and peak statistics). To specifically examine activation differences for counter-imitation when intentional compared with incidental, a T-contrast was calculated comparing intentional versus incidental mismatching conditions (cluster and peak statistics reported in table 8). Peaks within the bilateral insula cortices and SMA did indeed show significantly greater activation for intentional counter-imitation compared with incidentally mismatching actions (peak-level $p(\text{FWE}) < .05$). Furthermore, peaks within both the anterior and mid cingulate cortex were significantly more active for intentional compared with incidental counter-imitation.

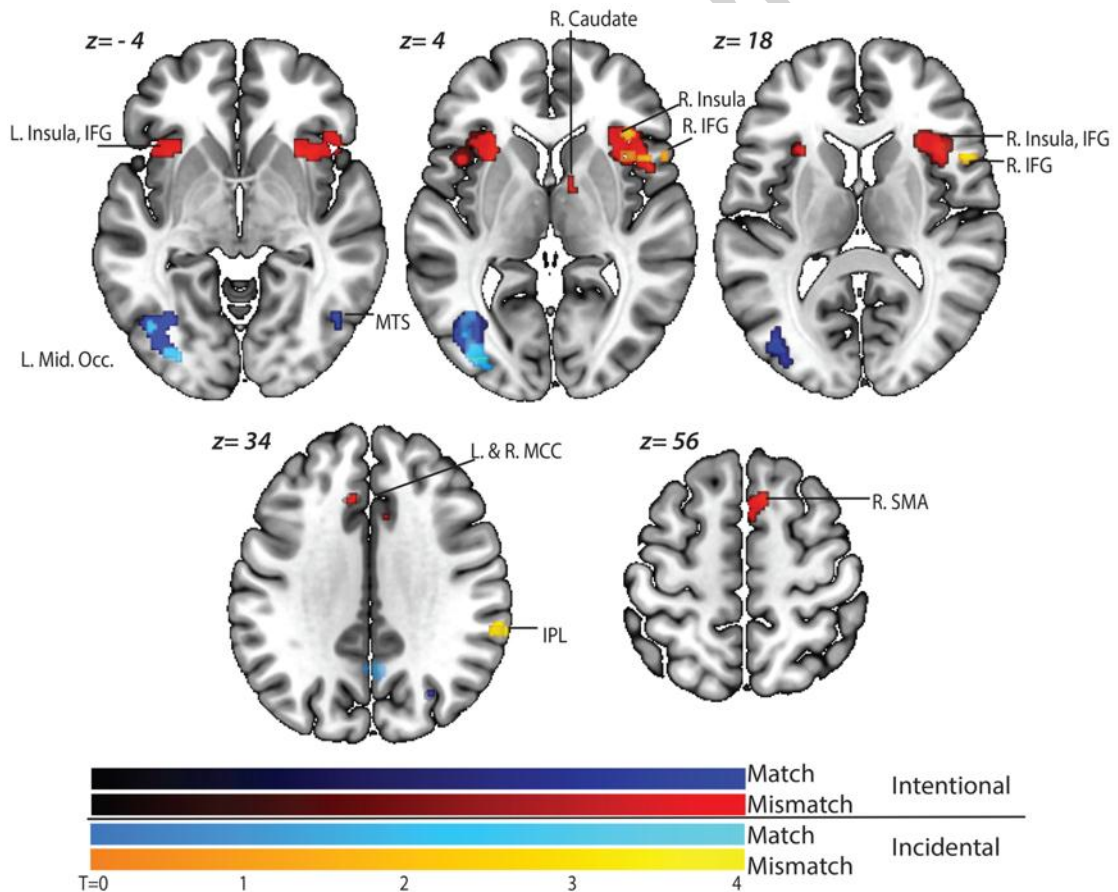


Figure 5. Brain areas showing significantly greater activation for matching versus mismatching actions, and vice-versa, for intentional and incidental conditions (z coordinates of axial slices)

indicated). Colour bars are displayed for each contrast, with height-threshold T indicated. All regions are displayed at peak-level $p(\text{FWE}) < 0.05$ except for the contrast of matching > mismatching in the incidental condition (light blue) which showed no significant voxels and is displayed here at peak-level $p(\text{uncorrected}) < 0.001$ with cluster-level $p(\text{FWE}) < 0.05$. Anatomical Abbreviations: IFG: Inferior Frontal Gyrus; MCC: Mid Cingulate Cortex; Mid. Occ.: Mid Occipital Cortex; IPL: Inferior Parietal Lobule; ITS: Inferior Temporal Sulcus; SMA: Supplementary Motor Area.

The clusters within insula cortices overlap with the areas showing a main effect of Congruency in the F-contrast (Figure 3, green clusters), suggesting that they are more active for mismatching compared with matching actions overall for both intentional and incidental conditions combined, reflecting the processing of stimulus-response *incompatibility*. We interpret the processing of such conflict as being linked to motor interference from a proponent tendency to imitate (Brass, et al. 2000, 2005; Kilner et al. 2003). Nonetheless, these bilateral clusters in the insula cortex were also significantly more active for mismatching actions when this is intentional rather than incidental, suggesting a specific role for intentional counter-imitation. In contrast, the cluster in the SMA overlaps with the area showing a significant main effect of Preparation Context in the F-contrast (Figure 3, yellow cluster), suggesting greater activation of the SMA when preparing responses that are relative to the stimulus (intentional copying or opposing conditions) than for performing a pre-specified action. Indeed, the SMA is known to be involved in motor planning more generally (Cunnington et al., 2005) and particularly when attention is focussed on intentions for action (Lau et al., 2004).

Table 4. T-contrast statistics for Intentional match > intentional mismatch

Cluster Statistics					Peak Statistics			
Label	% labelled	p(FWE)	k	x,y,z {mm}	Label	p(FWE)	T	Z
Inf. Occ.	71.5	<0.001	499	-42 -70 -2	Mid Occ.	<0.001	8.61	7.07
Fusiform	16.4			-34 -72 0	Mid Occ.	<0.001	7.32	6.27
Mid Occ.	9.4			-40 -78 8	Mid Occ.	<0.001	6.91	6
Mid Occ.	2	<0.001	52	-30 -88 22	Mid Occ.	0.003	6.03	5.38
Sup Occ.	2			-30 -78 22	Mid Occ.	0.01	5.71	5.15
Fusiform	16.7	0.006	6	-30 -42 -12	Fusiform	0.004	5.95	5.33
Mid Occ.	41.7	0.002	12	-28 -66 26	Mid Occ.	0.004	5.94	5.32
Inf. Temp.	56.1	<0.001	41	40 -68 -2	Mid Temp.	0.007	5.78	5.2
Mid Occ.	22			48 -66 -4	Mid Temp.	0.009	5.74	5.17
Mid Temp.	7.3							
Mid Occ.	16.7	0.006	6	36 -78 20	Mid Occ.	0.024	5.44	4.95
Mid Occ.	20	0.008	5	28 -70 32	Mid Occ.	0.027	5.4	4.92
Sup Occ.	100	0.027	1	-22 -74 30	Sup. Occ.	0.049	5.23	4.78

Notes: labelling via Automatic Anatomic Labelling (AAL) toolbox. Abbreviations: Inf. Temp.: Inferior Temporal Gyrus; Mid Occ.: Mid Occipital Gyrus; Sup. Occ.: Superior Occipital Gyrus

Table 5. T-contrast statistics for Intentional mismatch > intentional mismatch

Cluster Statistics					Peak Statistics				
Label	%labelled	p(FWE)	k	x,y,z {mm}	label	p(FWE)	T	Z	
Insula	8.2	<0.001	304	-30 22 2	Insula	<0.001	7.72	6.53	
IFG Oper	6.7			-38 20 -6	Insula	<0.001	6.72	5.87	
IFG Orb	5.3			-44 14 0	Insula	0.001	6.34	5.61	
IFG Tri	3.3								
Putamen	54.1	<0.001	540	34 22 8	Insula	<0.001	7.54	6.42	
IFG Tri	14.8			34 16 0	Insula	<0.001	7.31	6.27	
IFG Oper	13.9			42 16 4	IFG Oper	<0.001	7.17	6.18	
IFG Orb	13.7								
MCC	3.6	<0.001	28	10 18 36	MCC	0.002	6.22	5.52	
SMA	1.4	<0.001	70	4 14 56	SMA	0.002	6.13	5.46	
Caudate	87.5	0.001	16	10 2 6	Caudate	0.003	6.05	5.4	
MCC	409	<0.001	22	-8 26 32	MCC	0.004	5.98	5.35	
ACC	18.2								
Sup MFG	4.5								
Sup Frontal	4.4	<0.001	23	24 2 62	Sup Frontal	0.006	5.83	5.24	
Supramarg.					Supramarg.				
(IPL)	9.1	0.002	11	62 -38 36	(IPL)	0.014	5.6	5.07	
ACC	50	0.019	2	8 32 20	ACC	0.015	5.59	5.06	
SMA	100	0.027	1	12 10 68	SMA	0.047	5.24	4.79	

Notes: Cluster and maxima labels via Automatic Anatomic Labelling (AAL) toolbox. Abbreviations: ACC: Anterior Cingulate Cortex; IFG: Inferior Frontal Gyrus; IFG Tri.: IFG pars triangularis; IFG Orb.: IFG pars orbitalis; IFG Oper.: IFG pars opercularis; IPL: Inferior Parietal Lobule; MCC: Middle Cingulate Cortex; MFG: Medial Frontal Gyrus; Sup.: Superior; SMA: Supplementary Motor Area; Supramarg.: Supramarginal gyrus.

Table 6. T-contrast statistics for Incidental match > incidental mismatch[†]

Cluster Statistics					Peak Statistics			
Label	%labelled	p(FWE)	k	x,y,z {mm}	label	T	Z	p(unc)
Precuneus	62.8	0.017	153	-2 -56 22	Precuneus (left)	4.9	4.52	<0.001
				2 -58 30	Precuneus (right)	4.08	3.85	<0.001
				6 -52 20	Precuneus (right)	3.9	3.7	<0.001
Mid Occ.	83.5	0.032	131	-36 -84 0	Mid Occ.	4.5	4.2	<0.001
				-42 -68 0	Mid Occ.	3.98	3.76	<0.001
				-34 -84 -6	Mid Occ.	3.85	3.65	<0.001
				-40 -74 2	Mid Occ.	3.73	3.55	<0.001

Note: [†] FWE correction for multiple comparisons was applied at the cluster-level; deemed subthreshold. Cluster and maxima labels via Automatic Anatomic Labelling (AAL) toolbox.

Abbreviations: Mid Occ.: Mid Occipital Gyrus.

Table 7. T-contrast statistics for Incidental mismatch > incidental match

Cluster Statistics					Peak Statistics			
Label	%labelled	p(FWE)	k	x,y,z {mm}	Label	p(FWE)	T	Z
Mid Frontal	11.11	0.003	9	-28 34 24	Mid Frontal	0.002	6.22	5.53
Insula	7.1	0.001	14	38 16 0	Insula	0.003	6.08	5.42
Supramarg. (IPL)	3.45	<0.001	29	64 -40 32	Supramarg. (IPL)	0.005	5.88	5.28
SMA	8.3	0.002	12	10 10 66	SMA	0.005	5.88	5.28
IFG Oper	4.8	<0.001	21	54 14 12	IFG Oper	0.005	5.88	5.27
				46 14 6	IFG Oper	0.009	5.73	5.16
Insula	22.2	0.003	9	38 26 4	Insula	0.009	5.74	5.17
IFG Tri	11.1							
Insula	50	0.019	2	28 22 -8	Insula	0.022	5.47	4.97
IFG Oper	50	0.019	2	56 16 2	IFG Oper	0.035	5.33	4.86
Sup Temp	100	0.027	1	64 -40 16	Sup Temp	0.04	5.29	4.83
Cerebelum 6	50	0.019	2	-24 -68 -18	Cerebelum 6	0.042	5.27	4.82

Notes: Labelling via Automatic Anatomic Labelling (AAL) toolbox. Abbreviations: IFG: Inferior Frontal Gyrus; IPL: Inferior Parietal Lobule; Mid Frontal: Middle Frontal Gyrus; Sup.: Superior; SMA: Supplementary Motor Area; Supramarg.: Supramarginal gyrus; Sup. Temp.: Superior Temporal Gyrus

Table 8. T-contrast statistics for Intentional mismatch > incidental mismatch

Cluster Statistics					Peak Statistics			
Label	% labelled	p(FWE)	k	x,y,z {mm}	label	p(FWE)	T	Z
MCC	93.8	<0.001	144	-6 12 48	SMA	<0.001	7.52	6.41
SMA	3.5			-6 10 56	SMA	<0.001	6.75	5.89
Insula	24.1	<0.001	29	32 20 8	Insula	0.001	6.43	5.67
Insula	3.5	<0.001	29	-30 22 4	Insula	0.001	6.35	5.62
Precentral	16.7	0.006	6	-42 2 42	Precentral	0.006	5.83	5.24
MCC	6.3	0.001	16	8 22 36	MCC	0.007	5.8	5.22
ACC	5.9	0.001	17	-8 26 28	ACC	0.009	5.73	5.16
SMA	25	0.01	4	8 12 48	SMA	0.027	5.41	4.92

Notes: Cluster and maxima labels via Automatic Anatomic Labelling (AAL) toolbox.

Abbreviations: ACC: Anterior Cingulate Cortex; MCC: Middle Cingulate Cortex; SMA: Supplementary Motor Area.

4. CONCLUSIONS: TOP-DOWN CONTROL OF IMITATION

As hypothesised, performing an action that was incongruent with an observed action, either intentionally or incidentally, recruited regions of frontal control networks including the insula and cingulate cortices (Dosenbach et al., 2008; Mostofsky & Simmonds, 2008; Harding et al. 2015). Although this activation was observed for both intentional and incidental preparation contexts, recruitment of bilateral insula cortices and anterior and mid cingulate regions (as parts of the cingulo-opercular control network) was significantly greater for intentional counter-imitation than for incidental mismatching between observed and executed actions. This supports our hypothesis that frontal control processes distinguish intentional counter-imitation from incidental stimulus-response conflict or mismatch. Note that the cingulo-opercular network is considered to be related to stable task-set control, as distinct from more rapid, reactive adjustment of control (Dosenbach et al., 2008).

Cross and colleagues (Cross et al. 2013, 2014a, 2014b) have suggested that mirroring or imitation processes may be modulated by cognitive control processes, with the most convincing

evidence from their TMS study suggesting preparatory suppression of imitation-compatible motor responses during the preparation to intentionally counter-imitate (Cross and Iacoboni, 2014b). Our intentional counter-imitation condition is similar to that of Cross and Iacoboni's (2014b) task in which participants prepared to imitate or counter-imitate with different forewarning before the stimulus. By being able to examine the relationship between stimulus relevance, in intentional versus incidental conditions, and stimulus-response compatibility, in matching versus mismatching conditions, we are able to extend on this previous research to highlight the particular role of the bilateral insula and cingulate cortices in intentional counter-imitation. We therefore suggest that the insula and cingulate cortices, as part of the cingulo-opercular network, are involved in proactively inhibiting 'mirror' processing when intentionally counter-imitating.

The interaction effect we found between Congruence (match/mismatch) and the Preparation Context (intentional/incidental), highlighted peaks within the mid occipital cortex bordering on the inferior parietal lobule. This interaction was related to greater activation specifically for intentional imitation, when participants were forewarned to intentionally copy or imitate the observed action. We suggest that this represents greater recruitment of action observation processes when the task goal is specifically to imitate observed actions. Given that this is the only condition in which 'mirroring' of observed action is explicitly task-relevant, we suggest that this activation for intentional imitation may reflect an enhanced processing for observed actions, facilitating the performance of imitative responses.

Cross et al.'s (2013, 2014a; 2014b) proposal of preparatory facilitation and suppression of mirroring processes, when explicitly forewarned to imitate or to oppose observed actions, is complemented by the current findings. In particular we offer further support for insula and cingulate cortices being linked to intentional counter-imitation (Cross et al. 2013), and mid occipital and posterior parietal areas for intentional imitation (Cross et al. 2014a). Taken together these results provide support for the integration of higher-order control processes to regulate sensorimotor 'mirroring' depending on task demands.

In summary, the results reported here support the suggestion that mirroring and executive control processes work together to permit adaptive behaviour. For perception and action processes this is critical, given that the complexity of human interactions requires actions that are not only imitative. This work goes toward addressing a bias toward the over-simplification of action ‘mirroring’ processes in much of the earlier research on human mirror systems. Often non-imitative movements are overlooked, as well as the need to account for stimulus-response compatibility. Our actions also tend to be goal-directed, so control processes must guide how mirroring is employed to meet task demands. By manipulating both the task-relevance and the congruence of observed and executed actions we add to the emerging evidence for mirroring processes being integrated within broader functional systems for optimal control of complex behaviour.

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Conflicts of Interests

Nil.

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between action and perception. *Psych Res* 76(2): 171–182.

HIGHLIGHTS

- Control processes for intentionally imitating and counter-imitating were examined
- Congruency and task-relevance of observed and executed actions were manipulated
- Intentional counter-imitation recruited insula and cingulate cortices
- Intentional copying observed actions recruited posterior visual and parietal areas
- Results support the integration of cognitive control and mirroring processes