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The imitation game: Effects of social cues on ‘imitation’ are domain-general in nature

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ABSTRACT

Imitation has been hailed as ‘social glue’, facilitating rapport with others. Previous studies suggest that social cues modulate imitation but the mechanism of such modulation remains underspecified. Here we examine the locus, specificity, and neural basis of the social control of imitation. Social cues (group membership and eye gaze) were manipulated during an imitation task in which imitative and spatial compatibility could be measured independently. Participants were faster to perform compatible compared to incompatible movements in both spatial and imitative domains. However, only spatial compatibility was modulated by social cues: an interaction between group membership and eye gaze revealed more spatial compatibility for ingroup members with direct gaze and outgroup members with averted gaze. The fMRI data were consistent with this finding. Regions associated with the control of imitative responding (temporoparietal junction, inferior frontal gyrus) were more active during imitatively incompatible compared to imitatively compatible trials. However, this activity was not modulated by social cues. On the contrary, an interaction between group, gaze and spatial compatibility was found in the dorsolateral prefrontal cortex in a pattern consistent with reaction times. This region may be exerting control over the motor system to modulate response inhibition.

Introduction

Imitation – copying another's configural body movements – is a crucial component of skill learning and an important aspect of social and cognitive development. The social functions of imitation and the ensuing positive consequences of being imitated have been widely documented (see Chartrand and Lakin (2013) for a review). A group of prevailing theories propose that imitation can be used as a strategy to promote social standing and build rapport with others (Cook and Bird, 2011; Cook and Bird, 2012; Lakin et al., 2008; Lakin and Chartrand, 2003; Lakin et al., 2003; Leighton et al., 2010; Stel and Vonk, 2010; Wang and Hamilton, 2012). These theories predict that the social signals in any given situation should modulate the degree to which imitation is employed. For example, you may be more likely to imitate an individual when you have a goal to affiliate with them (Lakin and Chartrand, 2003), but less when faced with a person who has been stigmatised in some way (Johnston, 2002). Thus imitation has been hailed as a ‘social glue’ which enables us to effectively build and maintain social relationships (Lakin et al., 2003). However, a number of studies examining this strategic social modulation of imitation report mixed findings (Bourgeois and Hess, 2008; Mondillon et al., 2007; Rauchbauer et al., 2015; Yabar et al., 2006). Furthermore, the measurement of imitation has often been confounded with that of spatial compatibility, making it unclear whether social signals play a specific role in modulating imitation or a more general role in modulating attentional or response inhibition processes. Modulation of these processes might result in an apparent effect on imitation but in reality may be due to modulation of spatial compatibility. The current study therefore combines measurement of imitation and spatial compatibility to address the extent to which social information specifically modulates imitation, while using fMRI to examine the neural networks which implement this modulation.

Social modulation of imitation

Initial studies of the social modulation of imitation focused on group membership. It was predicted that individuals will have a stronger affiliation goal for those within their own social group compared to those in a different group, and will therefore imitate ingroup members to a greater extent than outgroup members (Lafrance and Broadbent,

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1976). However, literature on the modulation of imitation by social groups does not tell such a simple story. Although participants were more likely to exhibit behavioural mimicry for members of their ingroup in one study, compared to members of an outgroup (Yabar et al., 2006, Experiment 1), a follow-up experiment failed to replicate this effect (Yabar et al., 2006, Experiment 2) and suggested that the differential effect of group membership on imitation was driven by differences in the degree to which the outgroup was liked. This pattern is seen in other studies; while participants were more likely to imitate those with whom they share similar political attitudes (Bourgeois and Hess, 2008, Experiment 1), and when imitation partners shared a hobby of theirs, they did not show differential imitation of members of their own race vs a different race (Bourgeois and Hess, 2008, Experiment 2). Similarly, although Mondillon et al. (2007) showed that Caucasian participants imitated the facial expressions of other Caucasian models but not Chinese expressions, Chinese participants imitated the emotional expressions of both groups. A further study demonstrated that participants imitated the finger movements of a racial outgroup member *more* than those of a racial ingroup (Rauchbauer et al., 2015). In each of these cases, a similar mechanism has been proposed to explain opposite effects: we are compelled to affiliate with our ingroup, and therefore imitate more; or, we are driven to decrease social distance with members of an outgroup and therefore imitate more. This is problematic because it makes it very difficult to generate specific predictions about the direction of effects in such studies.

Contrary to the mixed effects of group membership on imitation, manipulating the gaze direction of the person being imitated can robustly modulate imitation (Wang and Hamilton, 2014; Wang et al., 2011a,b). Specifically, when the agent being imitated provides direct gaze to the imitator, imitation is enhanced (Wang et al., 2011a). Yet when the agent averts their gaze from the imitator, by either looking away, looking at their own hand, or if their eyes are occluded, imitation is reduced (Wang and Hamilton, 2014). Thus it seems that direct gaze is a powerful modulator of imitation.

The mechanism through which social factors modulate imitation is largely unknown. Two crucial questions relating to the mechanism can be distinguished. The first relates to the locus of the effect of social factors on imitation: whether social factors modulate input into the imitation system (by increasing visual processing of another's action), the imitation system itself (that which maps observed actions onto executed actions), or the output of the imitation system (via reduced response inhibition). The second question concerns the specificity of the effect of social factors on imitation. Thus far, most theoretical and empirical work on the social modulation of imitation assumes that the social features of an interaction have a direct and specific impact on imitation (Cook and Bird, 2011, 2012; Leighton et al., 2010; Rauchbauer et al., 2015; Wang et al., 2011a,b). It is possible that a mechanism exists specifically to modulate imitation on the basis of social cues, but it is also possible that the social modulation of imitation is due to a domain-general mechanism such as increased attention to stimuli, or the modulation of response inhibition allowing the expression of more automatic behaviours. In the example of group membership, individuals may be more likely to attend closely to their own social group compared to an outgroup, but this effect might also be reversed if an individual is motivated to pay more attention to the outgroup stimulus, for example due to perceived threat (Rauchbauer et al., 2015) or a desire to decrease the social distance between themselves and the outgroup member (Miles et al., 2011). Indeed, fMRI evidence suggests that direct eye contact serves to increase the activity of the superior temporal sulcus (STS; Wang et al., 2011b), a brain area involved in visual processing of biological motion, perhaps indicating greater visual analysis on trials in which direct gaze is present.

An effect of social modulation on response inhibition is of interest as both imitation-specific and domain-general hypotheses can be derived. Social modulation, whether by direct eye gaze or the use of ingroup models, may serve to reduce response inhibition such that any automatic behaviour is more likely to be exhibited, including imitative responses; or, effects may be specific to the inhibition of imitative or non-imitative behaviours. The latter possibility is made plausible by a recent body of work which suggests that inhibition of imitation relies on mechanisms at least partially distinct from those involved in the inhibition of other overlearned responses such as those indexed by the Stroop task (Brass et al., 2005; Hogeveen et al., 2014; Santiesteban et al., 2012a,b). At present it is difficult to determine the locus and specificity of the social modulation of imitation however, due to the fact that imitation has often been confounded with spatial compatibility.

Imitation or spatial compatibility?

The cognitive process unique to imitation involves the mapping of an observed action onto one's own motor repertoire (Brass and Heyes, 2005; Heyes, 2001). This mapping facilitates the reproduction of that same action in both speed and accuracy (Heyes, 2011). However, other visuospatial mappings can also produce similar effects on speed and accuracy: most relevant when considering imitation is the phenomenon of spatial compatibility, the tendency to respond more quickly and accurately to a stimulus when it appears in the same spatial location as the response (e.g. Simon, 1969). In many studies of imitation, it is possible that responses which appear to be imitative (i.e. due to mapping the observed action onto the motor program for the same configuration of body parts) could in fact be generated through spatial compatibility (i.e. due to mapping a stimulus in one spatial location onto a response using a body part in the same relative spatial location). For example, a participant may be asked to lift their right index or middle finger. Here, the index finger is on the left side of space and the middle finger is on the right. In many experiments, participants view the index and middle fingers of another person's left hand from a third-person perspective. In these stimuli, the index finger is on the left side of space and the middle finger is on the right. Participants are faster to lift their own index finger when the stimulus index finger lifts, than when the stimulus middle finger lifts. This effect may be due to the imitative *or* the spatial compatibility between stimulus and response. Due to the fact that most existing experimental paradigms confound spatial and imitative compatibility it is unclear whether social factors that appear to modulate imitation are indeed modulating the tendency to map another's action onto one's own motor repertoire, or instead are modulating the tendency to respond in the same spatial location as the observed action. The former is consistent with a specific effect of social factors on imitation, whereas the latter would suggest that social modulation of imitation is in fact the result of more general processes such as attention or response inhibition. In order to uncover whether apparent effects of social modulation are exerting their influence on imitation or on spatial compatibility, it is necessary to use a paradigm in which these two processes can be dissociated (Bertenthal et al., 2006; Boyer et al., 2012; Catmur and Heyes, 2010; Cooper et al., 2012; Sowden and Catmur, 2015; Wiggett et al., 2011). The use of such a paradigm in the present study allows the locus and specificity of social modulation effects on imitation to be determined. If social factors exert a general effect on attention to social stimuli one would expect both imitative and spatial compatibility to be modulated. If social modulation is specific to imitation, regardless of the locus of the effect of social factors, then one would expect imitative compatibility, but not spatial compatibility, to be modulated. If social factors modulate general response inhibition then imitative and spatial compatibility should both show modulation, unless the claim that control of imitation relies on mechanisms distinct from general inhibition is true, in which case effects on spatial compatibility alone are to be expected.

Neural mechanisms of imitation modulation

Imitation may rely on mirror regions (inferior parietal lobule, IPL and inferior frontal gyrus, IFG) of the human brain, which are active during both observation and execution of the same actions (Catmur et al., 2009; Heiser et al., 2003; Iacoboni et al., 1999; Kilner et al., 2009; Rizzolatti et al., 1999). A recent meta-analysis additionally implicates the superior parietal lobule (SPL) and dorsal premotor cortex in imitation (Molenberghs et al., 2009). Importantly, when an imitative response is inhibited, the temporoparietal junction (TPJ) and medial prefrontal cortex (mPFC) are additionally recruited (Brass et al., 2005). It is thought that these regions are instrumental in controlling imitative responses: the medial frontal region has been proposed as a candidate for the implementation of social modulation of imitation via direct gaze (Wang et al., 2011b). When imitation inhibition is required, top-down control from the medial prefrontal cortex is exerted over the superior temporal sulcus (STS), leading to reduced imitation (see STORM model for more information, Wang and Hamilton, 2012). Preliminary evidence indicates that neural substrates of the control of imitation and of spatial compatibility can also be distinguished, with stimulation to the right TPJ interfering with imitative responses, but leaving spatial compatibility effects intact (Hogeveen et al., 2014; Sowden and Catmur, 2015). However, a comparison of the neural networks that are engaged in modulating imitation and spatial compatibility has yet to be performed using neuroimaging techniques.

In the present study, we therefore re-examined the social control of imitation by group membership (which has previously shown mixed effects) and eye gaze (which has shown relatively stable effects). We examined the impact of these social cues on spatial compatibility in addition to imitation, using a design in which imitation and spatial compatibility effects can be dissociated and measured independently of one another. By using fMRI, we were also able to measure the neural locus of the effects of these social cues. We assessed the extent to which the neural networks implicated in the modulation of imitation serve this function specifically, or whether the same networks are involved in modulation of responding based on spatial compatibility.

During the experiment, participants were randomly assigned to one of two minimal groups before being asked to complete a finger lifting task during fMRI scanning. In this task, participants saw movies of an actress (either an ingroup or outgroup member) providing a gaze cue (direct or averted) before performing a finger lifting action. Simultaneously, participants were prompted to perform a finger lift that was either the same finger (imitatively congruent) or a different finger (imitatively incongruent) on the same side of space (spatially congruent) or a different side of space (spatially incongruent) to that shown in the movie. Reaction times to complete the finger lift, and neural responses during the task, were recorded. Compatibility effects (incongruent − congruent) were calculated for both imitation and spatial compatibility and the size of these compatibility effects under different group and gaze conditions were compared. We predicted that if social cues have a specific impact on the imitation system then imitative compatibility effects, but not spatial compatibility effects, should be modulated by social cues. Alternatively, if spatial compatibility effects, but not imitative compatibility effects, are modulated by social cues then it is likely that social cues are impacting automatic response inhibition. A scenario in which both imitative and spatial compatibility effects are modulated by social cues indicates an attentional mechanism can explain previous findings.

Materials and methods

Participants

Twenty-four right-handed participants (17 female, mean age = 23.71) took part. Data from a further five participants were collected but excluded due to technical errors with the scanner ($n = 3$), excessive head movement (>4 mm, $n = 1$), or identifying that the group manipulation was a sham ($n = 1$). Participants were recruited through the University of Surrey's research participation scheme and received £30 for participation. The study was approved by the University of Surrey ethics committee.

Stimuli and experimental design

Imitative and spatial compatibility effects were measured using a stimulus-response compatibility paradigm involving the observation and execution of finger lifting movements (Brass et al., 2001; Catmur and Heyes, 2010). The social modulation of each of these processes was assessed by combining hand stimuli with movies of either an ingroup member or an outgroup member giving the participant direct or averted gaze (see Fig. 1 and Supplementary Information for a description of how these movies were constructed).

Group membership (ingroup/outgroup), eye gaze (direct/averted), imitative compatibility (compatible/incompatible) and spatial compatibility (compatible/incompatible) were manipulated within-subject in a $2 \times 2 \times 2 \times 2$ factorial design. Mean trial duration was 3.9 s (500 ms Get Ready, 2400 ms Gaze Movie, 200–800 ms ISI, 500 ms Hand Movement) and was interspersed with a random jitter (Mean: 1000 ms, Range: 0–3000 ms, positive skew: 0.7). Participants completed 320 trials in a random order (16 trials per cell of the $2 \times 2 \times 2 \times 2$ design = 256 trials plus 64 neutral trials with an anonymous hand). All trials were completed in a single scanner run, lasting approximately 25 min. Eight 16 second rests were included periodically to give participants a break. During this time the word 'rest' appeared on the screen and participants were instructed to keep still.

Procedure

Before entering the scanner, participants completed a value-rating task which manipulated group membership. Participants were told that their ratings would be used to assign them to a group of people who shared similar values. In practice, participants were randomly assigned to one of two minimal groups, identified by a red or a blue background. To check the effectiveness of the group manipulation, participants then completed a battery of questions about their perceived fit to their group (see Supplementary information for methodological details and results). Participants also completed a 20-trial practice of the imitation task in which feedback was given.

Following scanning participants completed the questions about the groups again, to ensure the group manipulation was still present at the end of the study. In addition, participants also rated how much they liked the specific members of the two groups that they had seen and a third person that they had never seen before (see Supplementary Information for details and results). All stimulus presentation was coded in Matlab 2012 and presented with Cogent 2000.

Behavioural data analysis

Participants held down two keys with their right index and middle fingers throughout the experiment and responded to the imperative cue by releasing a key when making a finger lift. Reaction time to complete each finger lift was recorded throughout the task. Participant reaction times were trimmed (see Supplementary methods), means were computed for each cell of the design (see Supplementary results) and compatibility effects were calculated for each compatibility type (imitative compatibility: imitatively incompatible trials – imitatively compatible trials; spatial compatibility: spatially incompatible trials – spatially compatible trials). Imitative and spatial compatibility effects were submitted to two repeated measures 2 (group) × 2 (gaze) ANOVAs. Previous studies which do not control for spatial compatibility in this paradigm only analyse data from the two cells of the design in which both spatial and imitative compatibility are compatible or both are incompatible (indicated with a dashed border in Fig. 1B). To make these results comparable to previous studies, we also analysed these data in terms of this 'general compatibility', by calculating the general compatibility effect (spatially incompatible & imitatively incompatible trials − spatially compatible & imitatively compatible trials) which was also submitted to a 2 (group) × 2 (gaze) ANOVA. This general compatibility

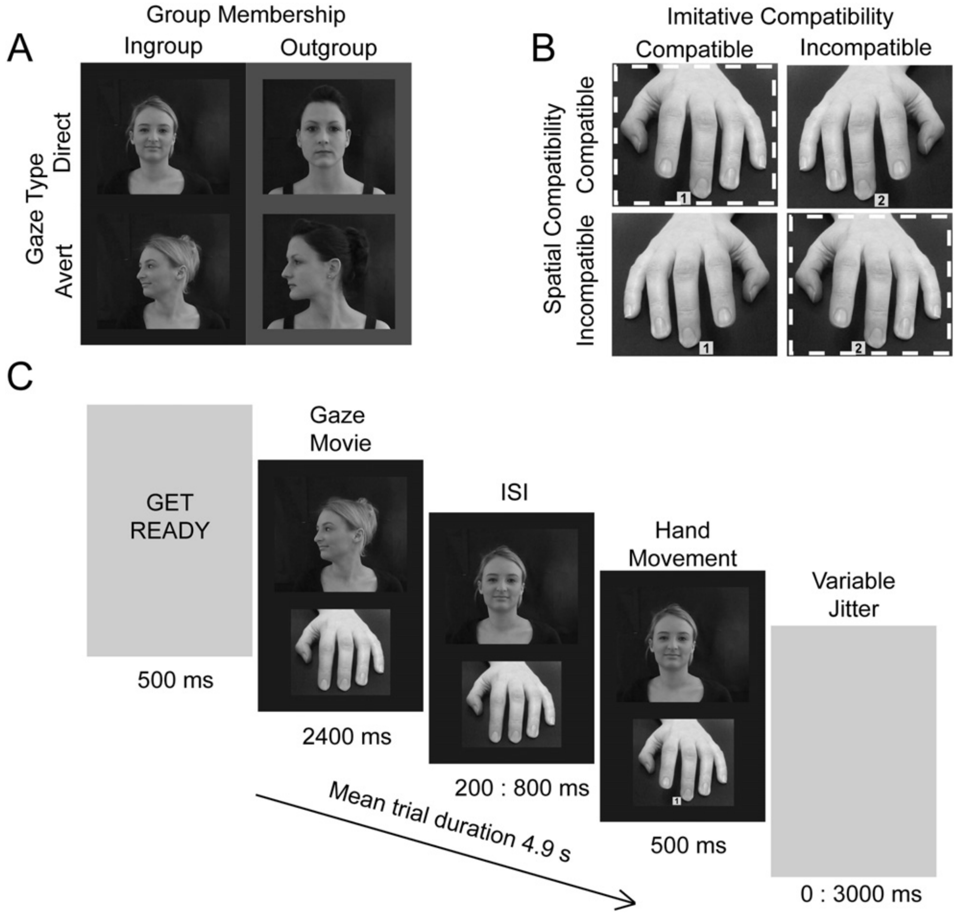

Fig. 1. Stimuli used in the present study. Panel A shows the final frames of the direct and averted gaze movies that remained on the screen during the imitation task. The shaded border denotes the group membership of the actress (in the experiment these were coloured red and blue; colour and identity was counterbalanced across participants). Panel B depicts each cell of the spatial and imitative compatibility design. The number appearing in the box between the index and middle finger is the imperative cue instructing the participant to lift either their index (cue = 1) or middle (cue = 2) finger. Dashed borders indicate the two cells of the design used to elicit the general compatibility contrast in which spatial and imitative compatibility were consistent (both compatible, or both incompatible). Panel C depicts the structure and timings of one trial in the study.

reflects the combination of both imitation and spatial signals as they would most often be experienced 'in the wild'. As there is no compatibility conflict within these trials (i.e. data from trials which are spatially compatible but imitatively incompatible and vice versa are removed from this analysis) we expect the general compatibility effect to be numerically greater than when examining spatial or imitative compatibility effects in isolation.

fMRI acquisition

Participants were placed supine in a 3 Tesla Siemens MRI scanner with a 32-channel phased-array head coil. During the experimental task, 25 axial slices were acquired using sequential acquisition (voxel size: 4 × 4 × 4 mm, matrix: 64 × 64, FOV: 25.6 cm) using a T2*-weighted EPI sequence (TR: 2000 ms, TE: 40 ms, flip angle: 85°). In total, 828 volumes were collected over the course of a single run. Following the experimental task, a high-resolution anatomical image was also collected using a T1-weighted MPRAGE sequence.

Pre-processing and GLM analysis

All pre-processing and analysis of the imaging data was completed using SPM12. Functional data were realigned and co-registered to the participants' anatomical image. To normalize the functional data, anatomical images were segmented using the standard tissue probability maps in SPM which generated a set of warps. These warps were then applied to the functional timeseries and 12 mm smoothing was applied. A design matrix was created for each participant with one regressor for each of the 16 experimental trial types and 4 additional regressors for each of the neutral trial types. Trials in which the participant made an erroneous response were modelled in a separate regressor and were not included in the analysis. Each trial was modelled as a stick function of 0 ms duration, corresponding to the onset of the imperative stimulus and convolved with the standard hemodynamic response function. Head movement parameters (six regressors) were also included.

To identify the brain regions engaged during the control of imitative and of spatial compatibility, two contrasts were computed across all conditions (spatially incompatible trials > spatially compatible trials, and imitatively incompatible trials > imitatively compatible trials). To make this experiment comparable to previously reported studies, a general compatibility contrast was also computed (spatially incompatible & imitatively incompatible trials > spatially compatible & imitatively compatible trials). To identify the regions which show the impact of social cues on imitative, spatial and general compatibility, contrasts were computed for the interactions between gaze type and each compatibility type, and group membership and each compatibility type. The three-way interactions between group, gaze and each compatibility type were also computed. All contrasts were taken to the second level for analysis and results are reported if they survived a voxel level threshold of $p = 0.001$ (uncorrected) with cluster level correction ($p = 0.05$ FWE).

Results

Behavioural results

Reaction times for each cell of the stimulus-response compatibility task are presented in supplementary table S1. Compatibility effects for imitative, spatial and general compatibility as a function of group identity and gaze type are presented in Fig. 2. Compatibility effects were analysed using repeated measures ANOVAs with factors of group (ingroup, outgroup) and gaze (direct, averted). One-sample *t*-tests were also performed to verify the presence of imitative, spatial, and general compatibility effects. Bayes' Factors (BF) are provided for all significant effects (BF_{10}, denoting strength of evidence for the alternative hypothesis over the null) and for all theoretically relevant null effects (BF_{01}, denoting strength of the null hypothesis over the alternative).

Effects of imitative compatibility

A one-sample *t*-test confirmed the presence of an imitative compatibility effect ($M = 10.4$ ms, $SEM = 2.7$ ms, $t(23) = 3.89$, $p < 0.001$, $d = 0.79$, $BF_{10} = 45.50$). The main effects of group and gaze on imitative compatibility, and the interaction between group and gaze, were not significant (main effect of group, $F(1,23) = 0.01$, $p = 0.94$, $\eta_p^2 = 0.00$, $BF_{01} = 4.73$; main effect of gaze, $F(1,23) = 0.01$, $p = 0.93$, $\eta_p^2 = 0.00$, $BF_{01} = 4.71$; interaction, $F(1,23) = 0.57$, $p = 0.46$, $\eta_p^2 = 0.02$, $BF_{01} = 3.22$).

Effects of spatial compatibility

A one-sample *t*-test confirmed the presence of a spatial compatibility effect ($M = 33.3$ ms, $SEM = 3.6$ ms, $t(23) = 9.23$, $p < 0.001$, $d = 1.88$, $BF_{10} = 3.509 * 10^6$). A significant interaction between group and gaze on spatial compatibility revealed a larger spatial compatibility effect during trials in which an ingroup member provided direct gaze and an outgroup member averted their gaze ($F(1,23) = 6.98$, $p = 0.02$, $\eta_p^2 = 0.23$, $BF_{10} = 4.69$). This interaction was driven by a larger spatial compatibility effect during trials in which an ingroup member provided direct gaze, compared to trials in which an outgroup member provided direct gaze ($t(23) = 2.98$, $p = 0.007$, $d = 0.61$, $BF_{10} = 6.80$); and also by a larger spatial compatibility effect during trials in which an outgroup member averted their gaze, compared to trials in which an outgroup member provided direct gaze ($t(23) = 2.74$, $p = 0.012$, $d = 0.56$, $BF_{10} = 4.24$). The main effects of group and gaze on spatial compatibility were not significant (main effect of group, $F(1,23) = 2.01$, $p = 0.17$, $\eta_p^2 = 0.08$, $BF_{10} = 0.50$; main effect of gaze, $F(1,23) = 2.54$, $p = 0.13$, $\eta_p^2 = 0.10$, $BF_{10} = 0.61$).

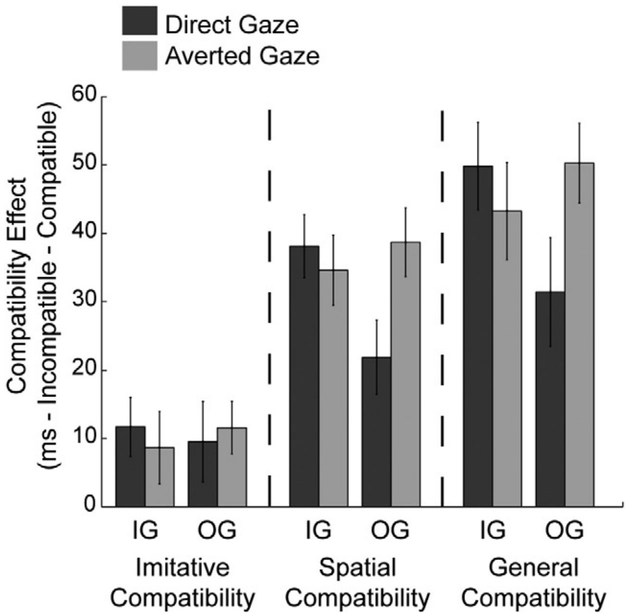

Fig. 2. Mean ± standard error of the mean compatibility effects (incompatible reaction time − compatible reaction time) as a function of group membership (IG − ingroup, OG − outgroup) and gaze for each compatibility type.

Effects of general compatibility

Data from the subset of trials which yielded a general compatibility measure (spatially & imitatively compatible vs. spatially & imitatively incompatible) were analysed in order to make these results comparable to studies in which imitation and spatial compatibility cannot be dissociated. A one-sample *t*-test confirmed the presence of a general compatibility effect ($M = 43.7$ ms, $SEM = 3.9$ ms, $t(23) = 11.07$, $p < 0.001$, $d = 2.26$, $BF_{10} = 8.936 * 10^7$). An interaction between group and gaze was also found on general compatibility, in a direction that is consistent with the effect on spatial compatibility ($F(1,23) = 5.80$, $p = 0.02$, $\eta_p^2 = 0.20$, $BF_{10} = 1.92$). This interaction was driven by a larger general compatibility effect during trials in which an ingroup member provided direct gaze, compared to trials in which an outgroup member provided direct gaze ($t(23) = 2.42$, $p = 0.024$, $d = 0.49$, $BF_{10} = 2.34$). The main effects of group and gaze on general compatibility were not significant (main effect of group, $F(1,23) = 0.92$, $p = 0.35$, $\eta_p^2 = 0.04$, $BF_{10} = 0.31$; main effect of gaze, $F(1,23) = 0.60$, $p = 0.45$, $\eta_p^2 = 0.03$, $BF_{10} = 0.32$).

fMRI results

Effects of imitative compatibility

Four brain areas responded more to the execution of imitatively incompatible finger lifts compared to imitatively compatible finger lifts (see Fig. 3, red and Table 1). These were right inferior parietal lobule (IPL), left temporoparietal junction (TPJ), anterior cingulate cortex (ACC) and a diffuse cluster with its peak in right inferior frontal gyrus (IFG) and extending to dorsal premotor cortex. No regions of the brain showed a pattern of responses which indicated that either group membership or direct gaze modulated imitative compatibility.

Effects of spatial compatibility

Large bilateral clusters in superior parietal, extending to IPL and right dorsal premotor cortex responded more to the execution of spatially incompatible actions compared to spatially compatible actions. A gaze by spatial compatibility interaction was found in the right dorsal premotor cortex in which BOLD activity increased during spatially incompatible trials with averted gaze. Finally, an interaction between group, gaze and spatial compatibility was identified in right dorsolateral prefrontal cortex (dlPFC) in which BOLD activity increased during incompatible trials in which an ingroup member averted their gaze and outgroup members directed their gaze towards the participant (see Fig. 3, green and Table 2).

Effects of general compatibility

Large clusters of activation in right primary sensorimotor cortex, extending to IPL and TPJ, in right premotor cortex, extending to IFG, in left TPJ and in right dlPFC were found when contrasting generally incompatible and compatible trials (see Fig. 3 for a plot of the overlap between these regions and those active during spatial and imitative compatibility and Table 3). As with spatial compatibility, an interaction between group, gaze and general compatibility was identified in right dlPFC. Again, BOLD activity within this region increased during incompatible trials in which an ingroup member averted their gaze and an outgroup member directed their gaze towards the participant.

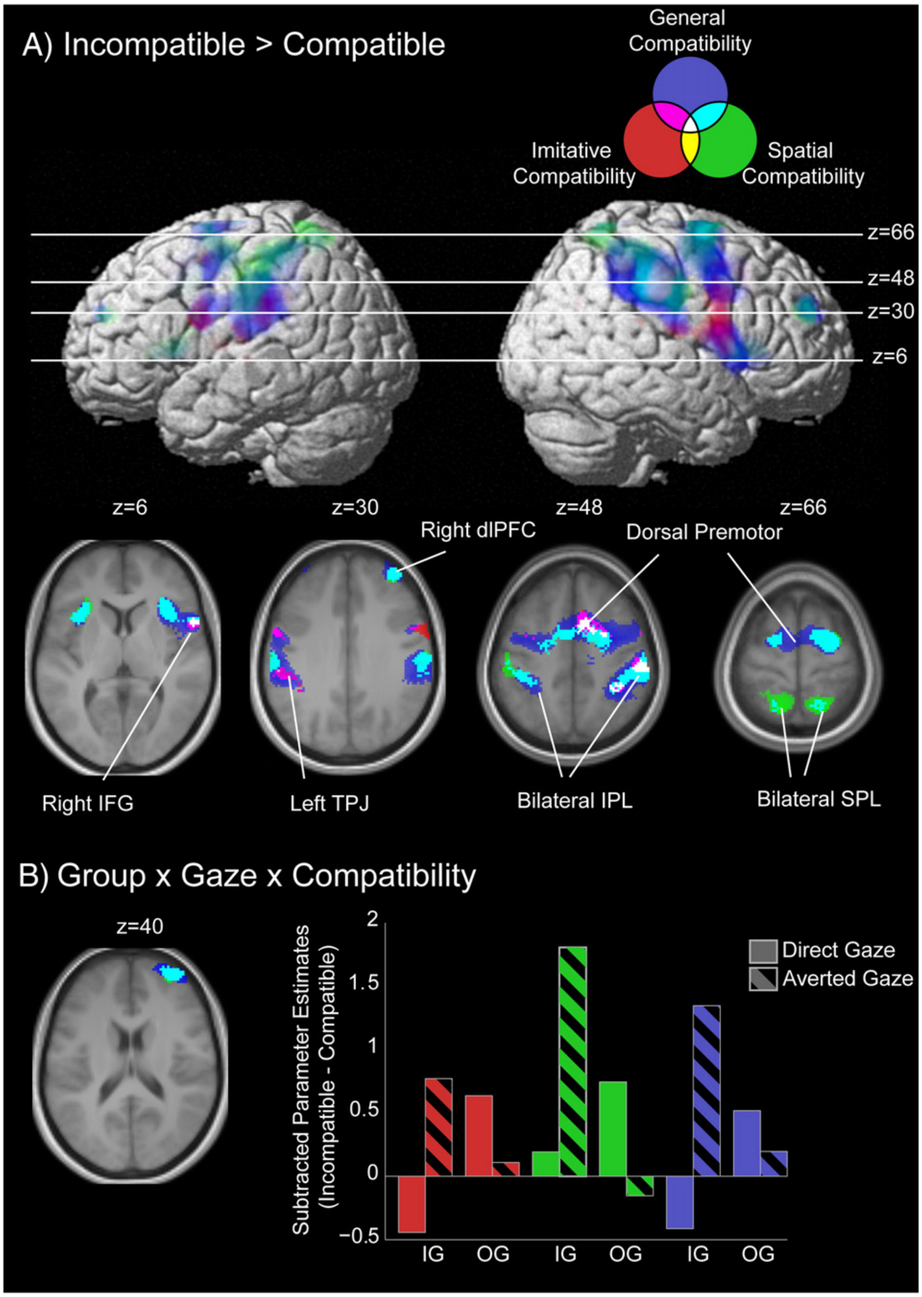

Fig. 3. fMRI results. Panel A shows whole brain compatibility effects for imitative (red), spatial (green) and general (blue) compatibilities. Overlap between these effects is shown in white. Panel B demonstrates the three-way interaction between group membership, gaze and compatibility for each compatibility type. Note that this three-way interaction is only significant for the spatial and general compatibilities. All figures are thresholded at $p < 0.001$ (uncorr) and $p < 0.05$ FWE cluster correction.

Discussion

The present study aimed to identify the mechanisms through which imitative responses may be modulated by social factors. It was investigated whether social factors affect imitation specifically, or whether they produce domain-general effects. In addition, the experimental paradigm allowed the locus of social modulation effects to be identified — whether inputs to, output from, or the imitation system itself is modulated.

Behavioural results

Imitation and spatial compatibility effects were evident in reaction times as participants were slower to perform incompatible responses in both domains. As the stimuli in this study allow us to dissociate the spatial and imitative components of the task, this provides further evidence that imitation is independent of spatial compatibility (Catmur and Heyes, 2010; Cooper et al., 2012). As in previous studies, we found that the compatibility effect driven by imitative compatibility was numerically smaller than that driven by spatial compatibility, and it seems that the general compatibility effect that is typically measured is an additive combination of the two.

An interaction between group membership and direct gaze on general compatibility revealed that direct gaze enhances the compatibility effect for the ingroup but decreases the compatibility effect for the outgroup. This finding is consistent with previous work which demonstrates that direct gaze enhances compatibility effects (Wang and Hamilton, 2014; Wang et al., 2011a,b) but also goes beyond this finding, demonstrating that the participant must also perceive the interaction

Table 1
Stereotaxic co-ordinates for contrasts examining imitative compatibility.

Location	p(FWE cluster corrected)	Size	T	MNI coords		
				x	y	z
Imitative compatibility (I > C)						
Right IFG	**<0.001**	**733**	**5.72**	**62**	**6**	**16**
Right dorsal premotor				62	6	34
Right IFG				52	8	24
Right IPL	**0.002**	**424**	**5.21**	**60**	**−26**	**42**
Right primary sensorimotor				50	−18	46
Left TPJ	**0.020**	**245**	**4.80**	**−50**	**−28**	**26**
Left TPJ				−44	−32	22
Left IPL				−42	−40	32
ACC	**0.014**	**300**	**4.35**	**10**	**12**	**48**
ACC				18	4	48
ACC				10	20	40
Group × Imitative compatibility						
No suprathreshold clusters						
Gaze × Imitative compatibility						
No suprathreshold clusters						
Group × Gaze × Imitative compatibility						
No suprathreshold clusters						

Table 3
Stereotaxic co-ordinates for contrasts examining general compatibility.

Location	p(FWE cluster corrected)	Size	T	MNI coords		
				x	y	z
General compatibility (I > C)						
Right primary sensorimotor	**<0.001**	**3423**	**7.89**	**56**	**−26**	**48**
Right IPL				64	−28	40
Right TPJ				52	−26	38
Right premotor	**<0.001**	**6968**	**6.45**	**30**	**0**	**48**
Right dorsal premotor				22	−4	66
Right IFG				56	12	6
Left TPJ	**<0.001**	**2803**	**5.63**	**−54**	**−32**	**30**
Left secondary sensorimotor				−54	−24	20
Left IFG				−60	4	26
Right dlPFC	**0.041**	**240**	**4.71**	**36**	**50**	**30**
Group × General compatibility						
No suprathreshold clusters						
Gaze × General compatibility						
No suprathreshold clusters						
Group × Gaze × General compatibility						
Right dlPFC	**0.013**	**510**	**5.21**	**40**	**60**	**2**
Right dlPFC				40	58	16
Right dlPFC				28	62	12

partner to be a member of their own ingroup for this effect to occur. If interacting with an outgroup member, participants showed the reverse pattern of results, with greater compatibility effects observed during averted gaze trials. These data are consistent with an approach-avoidance explanation in which direct gaze from a perceived ingroup member encourages approach behaviour (Mason et al., 2005), such as increased imitation, hypothesised to signal affiliation and likeness. In contrast, direct gaze from an outgroup member may be perceived as aggressive or threatening behaviour (Trawalter et al., 2008) and may lead to reduced imitation in an attempt to avoid engagement. This explanation is consistent with previously reported findings which do not explicitly separate the effects of spatial and imitative compatibility. However, examining the task elements which are driving this interaction, it becomes apparent that group membership and direct gaze are modulating spatial compatibility rather than imitative compatibility. This finding provides the first direct evidence that social cues do not specifically modulate imitation, and instead implies that a domain-general mechanism may be operating.

Furthermore, the pattern of modulation by group membership and eye gaze allows the nature of the domain general effect to be specified. An effect whereby group membership and eye gaze interact to modulate attention towards the stimulus would have produced modulation of both imitative and spatial compatibility. The selective modulation of spatial compatibility observed in these data is best explained by a model in which group membership and eye gaze interact to modulate general response inhibition, affecting the degree to which automatically-cued behaviour is expressed, but not the imitation-specific mechanisms identified by Brass et al. (2005) and Hogeveen et al. (2014). Future work should establish whether other forms of social cue have similar effects on spatial, but not imitative, compatibility: for example, using pro-social or interdependence priming may produce a different pattern of effects, possibly indicating a different underlying mechanism (Cook and Bird, 2011, 2012; Hogeveen and Obhi, 2011).

Table 2
Stereotaxic co-ordinates for contrasts examining spatial compatibility.

Location	p(FWE cluster corrected)	Size	T	MNI coords		
				x	y	z
Spatial compatibility (I > C)						
Left SPL	**<0.001**	**1354**	**5.99**	**−14**	**−58**	**68**
Left IPL				−56	−26	46
Left IPL				−38	−38	56
Right IPL	**<0.001**	**1985**	**5.99**	**56**	**−26**	**42**
Right SPL				20	−56	68
Right IPL				60	−32	38
Right dorsal premotor	**<0.001**	**2339**	**5.97**	**22**	**−4**	**66**
Right MFG				24	−10	58
Right SFG				−16	−6	54
Group × Spatial compatibility						
No suprathreshold clusters						
Gaze × Spatial compatibility						
Right dorsal premotor	**0.02**	**298**	**5.52**	**38**	**−10**	**64**
Right dorsal premotor				40	−24	54
Right dorsal premotor				25	−15	55
Group × Gaze × Spatial compatibility						
Right dlPFC	**0.049**	**264**	**4.51**	**30**	**56**	**24**

fMRI results

For the first time, these results allow the networks supporting the control of imitation to be measured alongside those involved in the control of spatial compatibility, within the same task and using the same stimuli. Results demonstrate some overlap, along with some separation, between networks for these processes. A right-lateralised network including the IPL, IFG and dorsal premotor cortex responded to both spatial and imitative compatibility. The network activated by spatial compatibility alone was bilateral, including these regions but additionally recruiting bilateral SPL and right dlPFC. The left TPJ on the other hand, responded to imitative compatibility alone. These results support the contention that the control of imitation recruits a network distinct from that involved in the control of other overlearned responses, and that the TPJ is a core node within this network (Brass et al., 2005; Santiesteban et al., 2015).

These results can also determine whether activity within the imitative and spatial compatibility control networks is modulated by the social factors of group membership and eye gaze. Only one region showed such social modulation – the right dlPFC – and, in accordance with the reaction time data, only as a function of spatial, not imitative, compatibility. In combination with the behavioural results, it seems that group membership and eye gaze modulate spatial compatibility but not imitation. Additionally, it seems that imitative control is governed by the TPJ which is not subject to such social modulation. In contrast, spatial compatibility recruits standard areas involved in cognitive control such as the dlPFC (MacDonald et al., 2000), which is subject to social modulation.

In addition to their internal coherence, the results observed here are consistent with previous demonstrations of the selective role of TPJ in the control of imitation (Brass et al., 2005; Hogeveen et al., 2014; Santiesteban et al., 2012a, 2015; Sowden and Catmur, 2015). It is notable however that activation of mPFC was not observed in response to the control of imitation, nor was its activity modulated by the social factors of group membership or eye gaze (even at reduced thresholds).

This is in contrast to previous studies (Wang et al., 2011a,b) although it is notable that a recent study investigating modulation of compatibility (the design made it difficult to determine whether results were due to imitative or spatial compatibility) by group membership and emotion also failed to find evidence of mPFC involvement (Rauchbauer et al., 2015).

In summary, the current study is the first to elucidate the mechanism through which social cues can modulate different types of automatic responding. We show that group membership and eye gaze both selectively modulate spatial compatibility, whilst having no effect on imitative compatibility. Furthermore, this modulation is associated with increased responding in the dlPFC which is indicative of increased cognitive control. This pattern of results indicates that social cues specifically modulate automatic response inhibition, rather than general attention or imitation-specific processes, at least in the type of task employed in this study.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.neuroimage.2016.06.050.

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