



The shared neural basis of empathy and facial imitation accuracy

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ABSTRACT

Empathy involves experiencing emotion vicariously, and understanding the reasons for those emotions. It may be served partly by a motor simulation function, and therefore share a neural basis with imitation (as opposed to mimicry), as both involve sensorimotor representations of intentions based on perceptions of others' actions. We recently showed a correlation between imitation accuracy and Empathy Quotient (EQ) using a facial imitation task and hypothesised that this relationship would be mediated by the human mirror neuron system. During functional Magnetic Resonance Imaging (fMRI), 20 adults observed novel 'blends' of facial emotional expressions. According to instruction, they either imitated (i.e. matched) the expressions or executed alternative, pre-prescribed mismatched actions as control. Outside the scanner we replicated the association between imitation accuracy and EQ. During fMRI, activity was greater during mismatch compared to imitation, particularly in the bilateral insula. Activity during imitation correlated with EQ in somatosensory cortex, intraparietal sulcus and premotor cortex. Imitation accuracy correlated with activity in insula and areas serving motor control. Overlapping voxels for the accuracy and EQ correlations occurred in premotor cortex. We suggest that both empathy and facial imitation rely on formation of action plans (or a simulation of others' intentions) in the premotor cortex, in connection with representations of emotional expressions based in the somatosensory cortex. In addition, the insula may play a key role in the social regulation of facial expression.

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Introduction

Facial expression is one of the most important ways in which people communicate. It involves expressions modified through social learning, and so develops through imitation involving the voluntary and intentional matching of behaviours (Bekkering et al., 2000; Wohlschläger et al., 2003). Imitation differs from mimicry which requires no modification of previously learnt behaviour (Provine, 2010; Yoon and Tennie, 2010) as it requires an understanding of the relationship between another person's actions, intentions and goals compared to one's own motor repertoire, to permit novel learning and expansion of a behavioural repertoire (Whiten, 2006). It follows that effective imitation of an emotional expression should require the observer to have some understanding of the relationship between the motor plan for the expression (Carpenter, 2006) and the underlying emotional state that the expresser may want to convey. In this sense, we would expect facial imitation to draw upon empathic mechanisms.

It has been suggested that both imitation (e.g. Leslie et al., 2004; Williams et al., 2007) and empathy (Gallese and Goldman, 1998)

involve the mirror neuron system (MNS; e.g. Rizzolatti et al., 1996). This action–perception matching mechanism is thought to be based in the inferior frontal gyrus (IFG), inferior parietal lobe and premotor cortex (Gallese et al., 1996; Molenberghs et al., 2012), though somatosensory cortex has also been implicated (Keysers and Gazzola, 2009). In a review of some 200 functional Magnetic Resonance Imaging (fMRI) studies that restricted its regions of interest to anterior intraparietal sulcus and premotor cortex, Van Overwalle and Baetens (2009) found that the MNS is engaged during perception or execution of articulated motions of body parts and argued that this confirms the self–other matching role of the MNS in understanding biological action. Therefore whilst there is little controversy as to whether the MNS plays a role in imitation, its role in empathy is much less clear. Meta-analyses of studies that elicit empathy during fMRI (Fan et al., 2011; Lamm et al., 2011) find consistent activation of the insula bilaterally, as well as the anterior dorsal and mid cingulate cortex extending into the supplementary motor area (SMA). They have not identified the MNS in empathic function in the absence of action observation (though SMA is arguably part of the human MNS since it has consistently been shown to be active during action observation and imitation – Caspers et al., 2010). Other reviews (Bastiaansen et al., 2009; Decety, 2011; Kurth et al., 2010) have also noted the importance of the insula and a lack of evidence for direct mirror system involvement in empathy. Nevertheless, some studies have implicated the MNS in empathy. Carr et al. (2003) found that

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both imitation and observation of emotional expressions activated premotor areas and suggested that we understand what others feel by a mechanism of action representation. Pfeifer et al. (2008) found a correlation between empathic traits in 10 year olds and inferior frontal gyrus activity during imitation. Cheng et al. (2009) found correlations between grey matter volume in mirror neuron areas and empathic traits, suggesting that the MNS is important for the development of empathic traits as well as imitation. Schulte-Ruther et al. (2007) asked participants to look at emotional expressions and ask ‘how do I feel?’ or ‘how does he feel?’ In voxels identified through a conjunction analysis of both conditions, the activity correlated with empathic traits in posterior Superior Temporal Sulcus (pSTS) as well as IFG.

The way that empathy is defined is relevant. It may be defined as the capacity to understand other people’s feelings and respond to them appropriately (Baron-Cohen and Wheelwright, 2004), though it is also appreciated to be a multifaceted concept (Decety, 2011), and many authors argue for categorising types of empathy. For example, whilst Baron-Cohen and Wheelwright (2004) proposed a single factor model of empathy that relies on both perception and understanding, Muncer and Ling (2006) identified 3 factors of cognitive empathy, emotional reactivity and social skills. In addition, empathic personality traits may be distinguished from empathy as a state of mind. De Vignemont and Singer (2006) restrict their definition of empathy to a conscious affective state that is isomorphic to another person’s affective state, elicited by the observation or imagination of that person’s affective state, with awareness that the other person is the source of this affective state. They see affect-sharing but not cognitive perspective-taking as essential to empathy. This framework has informed the design of those studies that have not found MNS involvement in empathy. However, this model of empathy is rather similar to that of emotional contagion (Hatfield et al., 1993), which in turn is akin to mimicry.

The processes involved in emotional contagion as a passive experience are likely different from more active attempts to understand what someone is feeling when they show novel or ambiguous behaviour. Then one can ‘simulate’ the other’s mental state (Gordon, 1996). Simulation theory of mind could be considered a descendant of ideomotor theory (Greenwald, 1970; James, 1890; Shin et al., 2010). This argues that the perception of an action ‘awakens’ the corresponding motor plan for that action, which, by drawing upon an experience of stimulus–response associations, can then be internally rehearsed without enacting, thereby enabling one to anticipate the next action in the sequence, predict what the other person is feeling and generate an understanding of intention. An ideomotor or simulation form of empathy is more akin to imitation, and thereby utilises sensorimotor representations which can be altered through new learning as actual outcomes differ from anticipated ones. In keeping with this argument, the studies cited above suggest that the human MNS becomes associated with empathy when tasks require more active engagement such as through imitation rather than just passive experience.

Behavioural studies of imitation ability have shown little in the way of a relationship with empathic traits. Two possible reasons for this may be considered. One is that imitation studies tend to explore manual actions rather than emotion. Secondly, those studies that do use emotional actions only examine imitation of stereotypical expressions, which do not place sufficient demand on those cognitive capacities that are specific to imitation. Studies of imitation have relied on the ‘do-as-I-do’ method of measuring imitation accuracy (e.g. Hamlin et al., 2008), whereby the amount of difference between the attempt and the model is quantified. While this approach is straightforward for simple and qualitatively distinct actions, everyday facial imitation is both emotionally communicative and demanding of subtle shifts in emotional expression. In theory, the Facial Action Coding System (FACS; Ekman and Rosenberg, 1998) could be used to deconstruct a facial action, but not only is it labour and time intensive, it describes an expression in terms of multiple variables making comparisons complicated. An alternative measure of imitation accuracy consists of examining whether

individuals show evidence of discrimination between subtly different actions by the way that they re-enact these demonstrated actions (Braadbaart et al., 2012; Williams et al., 2013b). For a series of actions, imitation accuracy can then be reflected by a rank correlation coefficient between the model and participant’s performance across trials.

We extended the principle of quantifying imitation accuracy to facial expression of emotion by designing a novel set of stimuli, using composites of the six basic emotions (happiness, fear, anger, surprise, sadness and disgust; e.g. Elfenbein and Ambady, 2002). These composites were created by systematically blending three basic emotional expressions in controlled proportions so that they formed two triangular arrays of 15 stimuli each (see Fig. 1 for example). This meant that each stimulus differed from each other by a quantifiable amount. Imitation accuracy could then be determined by how well photo-captures of imitation attempts allowed reconstruction of the original triangular expression arrays (see ‘Behavioural imitation tasks’ section). Williams et al. (2013a) used these emotional ‘blends’ to discover that the accuracy measure of emotional expression correlated with score on a self-report measure for empathy, the Empathy Quotient (EQ; Baron-Cohen and Wheelwright, 2004). The relationship between EQ and facial imitation ability could be explained in several ways. We hypothesised that facial imitation may serve as a proxy measure of empathy (Carr et al., 2003; Leslie et al., 2004), with both functions mediated by common cognitive control mechanisms based within the mirror neuron system (Bastiaansen et al., 2009; Decety, 2011; Iacoboni and Dapretto, 2006). Other mechanisms to consider were: (a) social motivation associated with the orbitofrontal cortex; (b) an inferential Theory of Mind mechanism based in the right temporoparietal junction and medial prefrontal

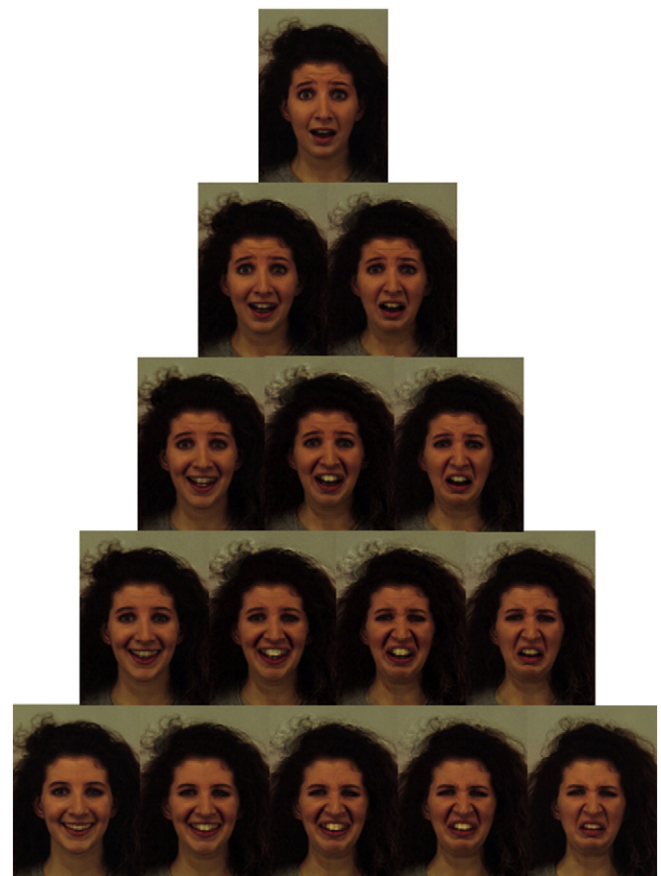


Fig. 1. Example of a Fear–Happiness–Disgust triangle, whereby the apices of the triangle show the three emotions expressed to 110%, and every other image represents increasingly mixed facial expressions, combining two or three emotions to create new images depending on the location of the image within the triangle.

cortex; (c) emotional perceptual sensitivity associated with the superior temporal sulcus and insula; and (d) language-based mechanisms.

The purpose of this study was to use fMRI to determine which brain areas mediated the relationship between imitation accuracy and empathic traits. First, we wished to know where Blood Oxygen Level Dependent (BOLD) signal activity during facial imitation correlated with variability in imitation accuracy. Second, we wished to know where activity during this task correlated with EQ. Areas where these two analyses overlapped would be the strongest candidates for mediating the imitation–empathy relationship found in the behavioural study. We hypothesised that this would include the “classic” mirror neuron areas, i.e. the inferior frontal gyrus, inferior parietal lobe and premotor cortex.

Methods

Participants

Twenty participants (10 female) between 19 and 45 years old were recruited, with a mean age of 26.3 (SD: 6.63). All participants were right-handed, and confirmed an absence of psychiatric disorder or history of illnesses that could affect the brain. Men were slightly older than women but not significantly so (male mean [SD] = 28.9[8.26]; female mean [SD] = 23.8[3.11]; $t = 1.830$, $df = 18$, $p = .084$). Empathy Quotient ranged from 20 to 62 (mean [SD] = 40.7 [9.31]) and gender differences were not significant (means [SD]: male = 36.8 [5.84]; female = 44.6; $t = 2.02$, $df = 18$, $p = .059$). EQ and imitation accuracy were normally distributed according to inspection of data and the Shapiro–Wilk test (EQ $p = .716$; accuracy $p = .146$). Age was non-normal ($p = .005$), so the logarithm of age was used in further analyses ($\log(\text{age})$ $p = .113$). The study was approved by the College Ethics Review Board of the University of Aberdeen.

Behavioural imitation tasks

Behavioural tests were performed before participants went into the MRI-scanner. Participants were first asked to fill in the Empathy Quotient questionnaire (Baron-Cohen and Wheelwright, 2004). Then, using a computer with camera, the participants were shown 30 different faces and asked to first study the face and then imitate its expression. Faces appeared for 6 s, after which a countdown informed the participant when their imitative attempt would be captured by a camera. Participants could see their own face next to each stimulus as seen through the camera, and were specifically instructed to look straight at the camera during the countdown, instead of at their own image. Participants started with a practice test consisting of 5 randomised stimuli from the set, after which the stimuli were shown in 3 blocks of 10 faces each. The 30 face stimuli originated from the Sadness–Anger–Surprise and Fear–Happiness–Disgust (Fig. 1) triangles as previously used by Williams et al. (2013a). The stimuli sets were designed to create a group of emotional expressions that were novel and differed from each other in a systematic way. Three faces at the apices of the triangular arrays represented the ‘basic emotions’ from the black-and-white Ekman face database (Ekman and Friesen, 1975) expressed to 110%. The 110% expressions were created using the “neutral” and “happy” expressions, for example, as endpoints of a transformation. Any expression can be transformed to add (or subtract) some amount of happiness; a “110% happy” image, therefore, is a caricature (Calder et al., 2000) of the “happy” expression, obtained by over-applying the difference between the “happy” and “neutral” expressions. Each face in the rest of the triangle was made up of blends of the emotions in the apices, where the amount of each corresponded to its geometric distance from the stereotyped expression at the apex. Therefore, the complexity of an expression increases as one moves towards the centre, with the sides of the triangle representing blends of two emotions, whilst those in the middle consist of blends of all three.

Facial imitation accuracy was derived by blind scoring. Without knowing what face the participants were trying to imitate, a scorer would attempt to recreate the original triangular array. The scorer viewed the 15 images that make up a triangle in a randomised triangular array, and then proceeded to move the position of the participant's facial expressions around so that it would best match the original array of stimuli. Once the scorer was satisfied that all images were in the right place, the participant's images were unmasked. Error was calculated by counting how many steps there were between the location in the triangle where the scorer had placed the participant's image and where it was actually supposed to be. The highest error score for any one image was therefore 4. Two scorers were used for the blind matching to minimise possible experimenter bias. The final imitation accuracy score was taken from the average error scores of the two raters after their second time rating the stimuli. Inter-rater reliability was confirmed with an intraclass correlation of .560 ($p < .05$). Repeated-measures Analysis of Variance (ANOVA) was used to investigate possible effects and interactions. Within-participant factors were the arrays of emotions (2 levels) and rater (2 levels). Sex was included as a between participant factors and age and EQ were included as a covariate.

MRI

MRI data was collected using a 3.0 T scanner (Achieva X-series, Philips Medical, Best, The Netherlands). A 32-channel phased-array head coil was used to obtain high resolution gradient echo 3D volumetric images and a set of functional images using Blood-Oxygen-Level-Dependent (BOLD) contrast. The head was firmly stabilised in the head coil before the start of the scanning session. The high-resolution images were collected using a T1 weighted sequence with the following parameters: field of view, 24 cm; 20/6, TR/TE; flip angle, 35°; slices, 124; slice thickness, 1.0 mm; matrix, 256 × 256. Functional MR images were acquired in the axial plane with a T2*-weighted single shot, gradient-echo, echo-planar pulse sequence with the following parameters: field of view, 24 cm; 2000/30, TR/TE; flip angle, 78°, slices, 30; slice thickness, 5 mm; matrix, 96 × 96. 260 images were acquired per run, with a total of 520 functional images acquired. To allow the magnetisation to reach equilibrium, 4 dummy scans were acquired at the start of each run. These were subsequently discarded. Structural images were reviewed by a clinical neuroradiologist to confirm the absence of any clinical abnormality.

Functional imaging task

Consistent with a tradition of imitation research comparing imitative to instructional praxis, we designed our experiment to compare an imitated facial expression to one performed in response to specific instruction. We also sought to match the low-level motoric and perceptual demands of both conditions, as well as the emotional content of stimuli, so that any differences between conditions could not be simply ascribed to differences in stimulus-induced effects of emotional stimuli. After the structural scan, participants received instructions reminding them of the task. On a screen they were presented with faces on a black background using Presentation (version 14, www.neurobs.com). Above each face was a white letter; either an I, an O or a T. Whenever the participant saw an I, they imitated the face they were seeing. When they saw an O or a T, they formed an ‘O’ with their mouth or stuck out their tongue, respectively. Task compliance was monitored with an MRI-compatible camera mounted on the head coil so that at least the mouth area of each participant was visible. The scanner stimuli were adapted from two sets of face identities taken from the Karolinska database (Lundqvist et al., 1998) to form a male and female version of the same two triangles that the participants imitated outside the scanner, but in colour (see Fig. 1). Nine faces were selected from each triangle; the three original emotional stimuli at the apices, the 50/50 mixes of two emotional expressions, and the three different blends of all

three emotions, resulting in 36 different stimuli in total. Each face was shown for 2 s, with a black screen shown in-between each stimulus. Timing between stimuli was jittered. One run consisted of 32 Mismatched (O and T) and 96 Imitate instructions, shown in randomised order, taking 8.6 min in total. There were two runs. The 96 imitation stimuli were subdivided so that there were equal amounts of single, two-mixed and three-mixed stimuli.

fMRI analysis

Functional MRI data was analysed using MATLAB software with SPM8 (<http://www.fil.ion.ucl.ac.uk/spm/software/spm8/>). The 260 functional images for each run were realigned to the first image of the run (see Supplementary material for post-hoc comparison of 5 mm/degrees versus 3 mm/degrees movement limits). The mean scan from realignment was co-registered to the T1, and the T1 segmented. Scans were then normalised to the T1 grey matter image using the standard SPM MNI template and smoothed with an 8 mm FWHM Gaussian kernel. The smoothed images were modelled using a General Linear Model, combining the two runs. The onset of each stimulus was assigned to either Imitate or Mismatch control (duration = 0 s), according to the relevant symbol, to generate t-tests. A standard high-pass filter was employed with 128 s cut-off, using the movement data from realignment as a regressor of no interest.

To make inferences at the group level, activation patterns from the individual t-tests were averaged across the 20 participants. This revealed the difference in activation between Imitate and Mismatch. EQ and facial imitation accuracy were then used as correlates in a multiple regression analysis with Imitate > Mismatch to reveal which brain areas were modulated by the differences in behavioural scores across participants. Additional analyses looked at differences in response to female versus male face stimuli, and the effects of the different emotions, to investigate whether there were any interacting effects of stimulus type on the data. All group results employed a voxel threshold of $p < .001$, with a cluster extent threshold of 38, derived from Monte Carlo simulations (Slotnick et al., 2003), which left only the clusters that were considered significant at an FWE-corrected threshold of $p < 0.05$. The Talairach atlas and AAL toolbox were used to define anatomical regions.

To determine whether head movement might have been greater in one condition compared to another, paired t-tests were performed on the realignment parameter data and are shown in Table 1. This suggested a difference for the amount of translational movement in the z-axis. However, given that the difference was less than 0.1 mm, was not significant with a Bonferroni correction for multiple comparisons, and that we employed head movement as a regressor anyway, we did not consider that this would have a meaningful effect on our results.

In order to find out where in the brain activation during imitation correlated with both EQ and accuracy, the group contrast for EQ correlated to Imitate > Mismatch was saved as a binary mask. This mask was then inclusively applied to the accuracy group correlation contrast, with the same threshold, to reveal where activation overlapped. The opposite analysis was performed (using the accuracy correlation as a mask) to double-check the results. Results were further confirmed by overlapping both binary masks in MRICroN (<http://www.mccauslandcenter.sc.edu/mricro/mricron/index.html>).

Table 1
Effects of task on movement parameters.

| Parameter | Mean difference (Imitation-Mismatch) | Std. deviation | t (df = 19) | Sig. (2-tailed) |
|-----------------|--------------------------------------|----------------|-------------|-----------------|
| X (mm) | -.00731 | .07670 | -.426 | .675 |
| Y (mm) | -.02647 | .10467 | -1.131 | .272 |
| Z (mm) | .06495 | .12143 | 2.392 | .027 |
| Pitch (degrees) | .00074 | .00250 | 1.331 | .199 |
| Roll (degrees) | .00027 | .00189 | .638 | .531 |
| Yaw (degrees) | .00039 | .00117 | 1.516 | .146 |

Results

Behavioural results

Effects of log(age), gender, rater and emotion-triangle were investigated with Repeated-measures ANOVA ($df = 16$). This revealed a main effect of EQ ($F = 7.72$, $p = .013$ $\eta^2 = .325$) but no significant effects of sex ($F = 1.32$, $p = .267$ $\eta^2 = .076$) or age ($F = 2.42$, $p = .140$ $\eta^2 = .131$), and the raters' scores did not differ significantly from each other ($F = 3.43$, $p = .082$ $\eta^2 = .177$). The only positive interaction effect found in the ANOVA was between triangle and EQ ($F = 5.23$, $p = .036$, $\eta^2 = .246$).

To find out which triangular array was responsible for the interaction effect, the relationships between EQ, triangle and accuracy were further investigated with a correlational analysis. This revealed that the correlation between EQ and the error score on the Fear–Happiness–Disgust triangle was highly significant ($r = -.740$, $p < .001$) whereas that of the Sadness–Anger–Surprise triangle was not ($r = -.151$, $p = .526$). There was no significant difference between error scores on the two triangles, which implies that they were equally difficult. Overall, EQ correlated significantly with error ($r = -.564$ with $p = .010$; Fig. 2); the negative correlation reported here indicates that accuracy and EQ are positively correlated.

Group BOLD activation

There was no main effect of gender (either participants' or stimuli) on brain activation. Relatively few effects of Imitate > Mismatch were found in the bilateral middle/inferior occipital gyri and right fusiform gyrus as shown in Table 2. In contrast, Mismatch > Imitate (Fig. 3 & Table 2) revealed multiple areas of highly significant activation.

Correlates with EQ

EQ correlated significantly with Imitate > Mismatch in a number of areas. There was a positive correlation in the right hippocampus (10 – 40 8), intraparietal sulcus (Brodmann Area (BA) 40; 32 – 40 38), bilateral precentral gyrus (premotor cortex; BA6; – 28 – 18 60 & 26 – 16 58) and right primary somatosensory cortex (38 – 20 34, 16 – 32 62 & 44 – 22 50), as shown in Fig. 4 and Table 3. A negative correlation between EQ and Imitate > Mismatch was also found, located in the bilateral cuneus (16 – 80 34 & – 14 – 84 28) and angular gyrus (– 40 – 46 24).

Correlates with facial imitation ability

The facial imitation accuracy score correlated positively with Imitate > Mismatch in the bilateral precentral gyrus (premotor and motor cortex), cerebellum, right thalamus, lentiform nucleus, insula,

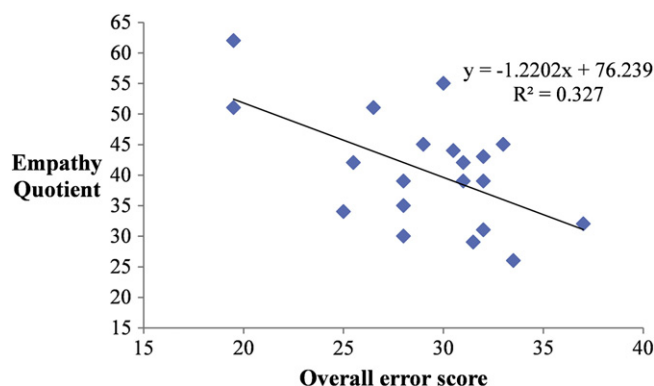


Fig. 2. Correlation between empathy and facial imitation error.

Table 2

Areas of significance identified in contrasts between Mismatch and Imitate conditions ($p < 0.001$ corr. with $k > = 38$), MNI-coordinates in mm (BA = Brodmann area).

| Brain region | Cluster size | T | Z-score | x | y | z |
|---|--------------|-------|---------|-----|-----|-----|
| <i>Mismatch > Imitate</i> | | | | | | |
| Bilateral insula (right side peak) | 24999 | 10.17 | 5.88 | 38 | −8 | −6 |
| Right precuneus | | 9.54 | 5.71 | 8 | −66 | 34 |
| Right middle temporal gyrus (BA21) | | 9.38 | 5.67 | 66 | −20 | −10 |
| Right superior frontal gyrus (BA6) | 1170 | 7.97 | 5.22 | 20 | 12 | 48 |
| Right ventromedial frontal cortex (BA8) | | 7.83 | 5.17 | 32 | 26 | 50 |
| Anterior cingulate (BA25) | 285 | 5.41 | 4.16 | 0 | 8 | −4 |
| <i>Imitate > Mismatch</i> | | | | | | |
| Left inferior occipital gyrus (BA19) | 55 | 5.43 | 4.17 | −36 | −90 | 0 |
| Right middle occipital gyrus (BA18) | 198 | 5.28 | 4.09 | 34 | −86 | 16 |
| Right fusiform gyrus | 114 | 4.89 | 3.89 | 48 | −66 | −14 |
| Left inferior occipital gyrus (BA19) | 90 | 4.87 | 3.88 | −34 | −88 | −14 |

somatosensory cortex and cingulate (see Fig. 5 & Table 4). There were no areas of significant activation where accuracy correlated negatively with Imitate > Mismatch.

Overlap between empathy- and ability-related brain activations

The only region where activation in the EQ and accuracy correlations with Imitate > Mismatch overlapped significantly was in the precentral gyrus (premotor cortex; BA6), with peak MNI-coordinates $x = -27$, $y = -17$, $z = 65$. This activation of the premotor cortex, as found through the SPM analysis, was further confirmed by overlaying the binary maps in MRIcroN (Fig. 6).

Discussion

The behavioural data replicated a previous finding from our research group of a correlation between imitation accuracy and empathy as

measured by EQ. To determine the mechanism mediating this relationship, we sought to identify where brain activity correlated with both EQ and imitation accuracy when the task was performed in an fMRI environment. In line with our main hypothesis, we found that EQ was positively correlated with activity in the intraparietal sulcus, premotor cortex and somatosensory cortex during Imitate relative to Mismatch, areas considered to be part of the ‘mirroring network’ (Keysers and Gazzola, 2009; Van Overwalle and Baetens, 2009). The right hippocampus was also implicated, but not the inferior frontal gyrus. Similarly, facial imitation accuracy correlated positively with the cortical and sub-cortical motor control structures that included the premotor and somatosensory cortices, as well as the thalamus, cerebellum and right insula. Only activity in the left superior premotor cortex was associated with both greater empathy and increased accuracy.

Group activation differences

To interpret the results, other findings need to first be considered. In contrast to previous studies that included only passive viewing as control conditions (Carr et al., 2003; Leslie et al., 2004), we found little greater activity in our imitation condition relative to our active control, though we found marked effects in the opposite contrast in bilateral insula, superior frontal gyrus, medial prefrontal cortex, and anterior cingulate. These effects are both suggestive of greater executive demands as well as greater effects of emotional contagion or mimicry in the control condition (Fan et al., 2011; Kurth et al., 2010; Lamm et al., 2011; as discussed in the Introduction). They are consistent with inhibition of a prepotent copying response (i.e. mimicry) during the control task which was not required during imitation. A perception–action mismatch was an inevitable consequence of having a non-imitative condition with low-level perceptual and motoric demands similar to the imitative condition, but without the self–other matching element, and it might be argued that a mimicry response would be greater in the control task. However, Brass and Heyes (2005) found activity during a mismatch for manual actions to be mainly associated with activity reflecting greater demands of self–other distinction in parietal cortex,

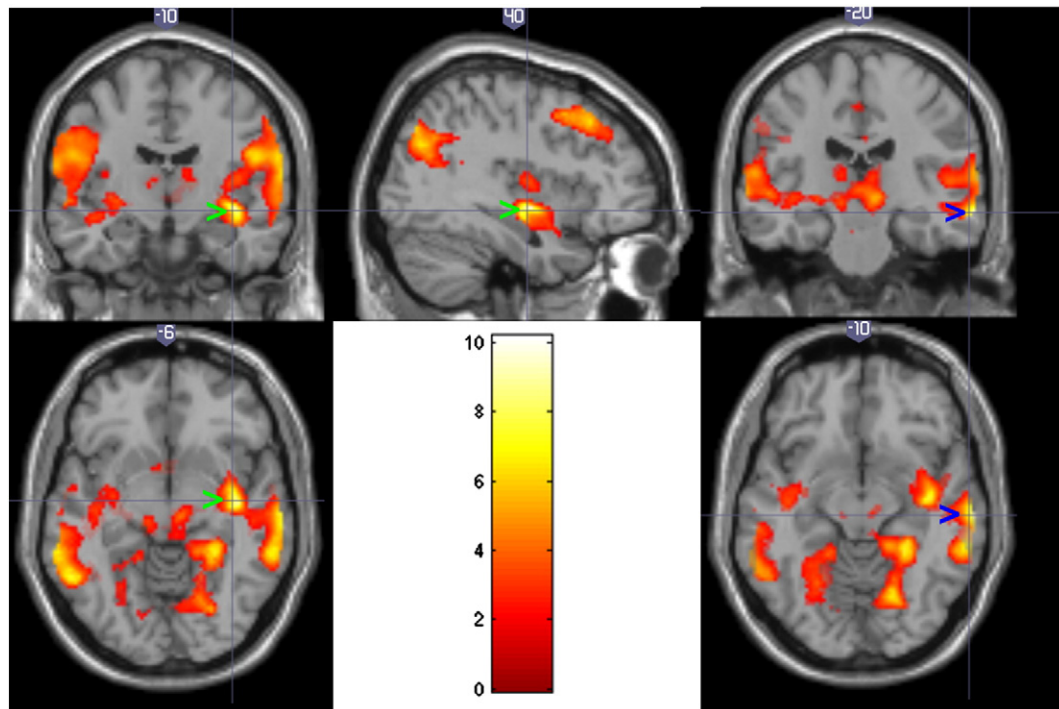


Fig. 3. Areas with a significant Mismatch > Imitate difference across participants. Significant activations occurred around insula ($x = 38$, $y = -8$, $z = -6$; green arrow) and middle temporal gyrus ($x = 66$, $y = -20$, $z = -10$; blue arrow) for 20 participants, at $p < .05$ FWE-corrected. Although Table 2 indicates that these areas belong to the same cluster, this figure illustrates that they represent distinctly different areas of significant activation.

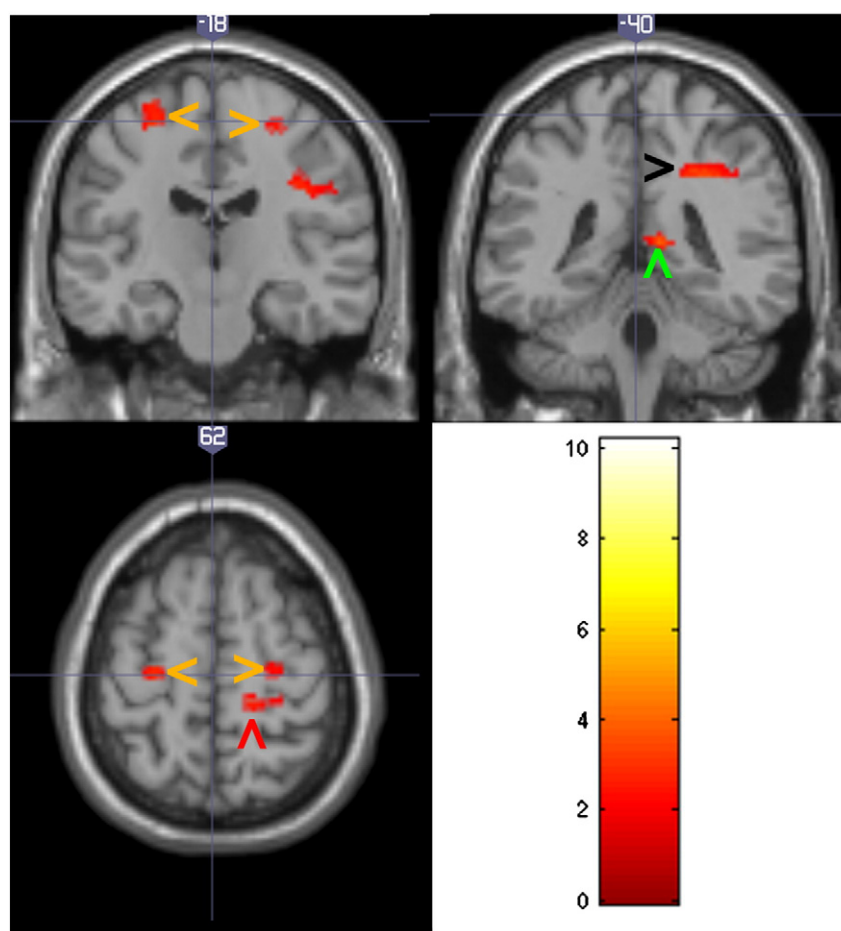


Fig. 4. Activation in Imitate > Mismatch positively correlated with EQ, at $p < .05$ FWE-corrected for 20 participants. Orange arrows indicate precentral gyrus, black = intraparietal sulcus, green = hippocampus and red = somatosensory cortex.

rather than inhibition, suggesting little in the way of a prepotent imitative response in their study. Our findings are therefore quite different, suggesting that facial stimuli are more effective at eliciting a mimicry type of response than manual stimuli.

Although mimicry goes some way to explaining insula and cingulate activity during the control task, one would expect equal levels of emotional contagion in mimicry and imitation and so it does not explain greater activity in the control task. One possible explanation is the known role of the anterior insula in the detection of action–response conflict (Ullsperger et al., 2010). Given additional evidence that the insula is involved in both visually perceived facial expression and self-expression feedback (Carr et al., 2003; Wicker et al., 2003), it is unsurprising that it should respond strongly to a mismatch between

perceived and enacted facial stimuli. It then follows that if the insula is an essential component of the error monitoring system, we would expect larger responses during imitation to result in greater error sensitivity and consequently higher accuracy, which is consistent with our accuracy–imitation findings. These results are consistent with models of imitation that describe it as a form of motor learning, relying on feedback error, to modify existing programmes, in order to achieve greater fidelity (Wolpert et al., 2003). We would therefore suggest that the insula plays a major role in the learning of facial expression, and therefore imitation of facial expression, at the level of action–perception mismatch detection.

The area of middle temporal gyrus that we identified has been shown to become active during reading (Price et al., 1994) and so can be explained by the fact that participants could rely solely on the instruction cue to select the correct action to execute in the Mismatch condition and consequently put greater emphasis on reading rather than on the face. This sort of explanation could also account for greater activity in the occipital gyrus for imitation, where participants were more reliant upon processing facial features to generate their responses. The lack of significant difference in inferior temporal gyrus or posterior superior temporal sulcus activation between the two conditions however precludes the notion that activation differences might have been solely driven by differences in visual input (e.g. Haxby et al., 2000).

Neural correlates of empathy and accuracy

The absence of activation differences in mirror neuron areas during imitation can be understood if the extra demands for imitation were negligible. If congruence between perception and action is detected

Table 3

Significant areas of correlation between EQ and Imitate > Mismatch ($p < 0.001$ corr. with $k > = 38$), MNI-coordinates in mm (BA = Brodmann area).

| Contrast | Brain region | Cluster size | T | Z-score | x | y | z |
|----------|-----------------------------------|--------------|-------|---------|-----|-----|----|
| Positive | Right hippocampus | 44 | 5.225 | 4.024 | 10 | −40 | 8 |
| | Right intraparietal sulcus (BA40) | 176 | 4.941 | 3.878 | 32 | −40 | 38 |
| | Left precentral gyrus (BA6) | 71 | 4.497 | 3.634 | −28 | −18 | 60 |
| | Right somatosensory cortex | 115 | 4.444 | 3.604 | 38 | −20 | 34 |
| | Right precentral gyrus (BA6) | 71 | 4.406 | 3.582 | 26 | −16 | 58 |
| | Right somatosensory cortex | 45 | 4.324 | 3.534 | 16 | −32 | 62 |
| | Right somatosensory cortex | 39 | 4.006 | 3.343 | 44 | −22 | 50 |
| Negative | Right cuneus | 118 | 4.852 | 3.830 | 16 | −80 | 34 |
| | Left cuneus | 93 | 4.533 | 3.655 | −14 | −84 | 28 |
| | Left angular gyrus | 55 | 4.259 | 3.496 | −40 | −46 | 24 |

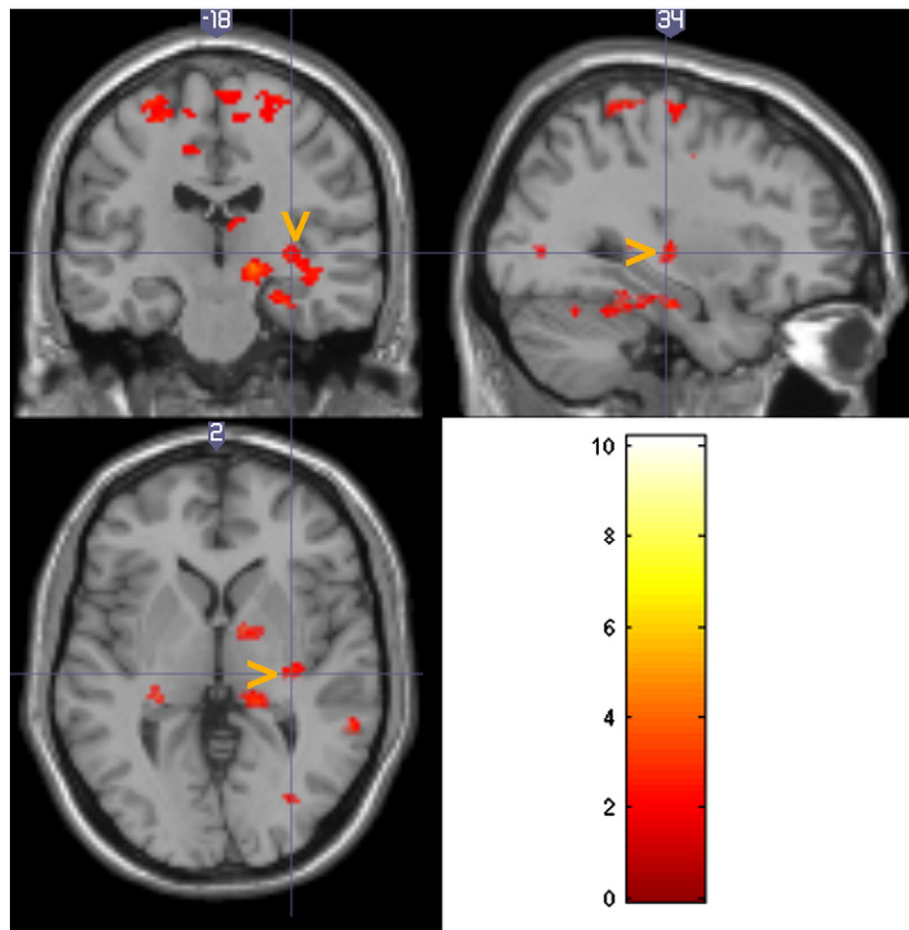


Fig. 5. Significant areas of positive correlation between Imitate > Mismatch and facial imitation accuracy ($p < .05$ FWE-corrected). Arrow indicates peak of the insular activation (crosshair on peak with $x = 34$ $y = -18$ $z = 2$). Other areas that are clearly visible on the transverse slice are thalamus (posterior and to the left of the insula) and globus pallidus (anterior to both insula and thalamus), with the precentral gyrus visible on the coronal and sagittal slices (red = least activated, white = most).

only by mirror neurons, which just make up a small percentage of the neuronal population (only about 6% of neurons in macaque F5 premotor cortex showed strict congruence in Gallese et al., 1996), the signal may be too weak to detect at a whole brain level. However, a small difference could be detected if it contributes substantially to variance in performance or a behavioural trait. This is consistent with our finding that the mirror neuron system was implicated in our correlational analyses; the intraparietal sulcus in the correlation between imitation and EQ, and the premotor and somatosensory cortices in both the accuracy and EQ correlations. While the inferior frontal gyrus, which was not implicated

Table 4

Areas of significant correlation between accuracy and Imitate > Mismatch ($p < .001$ with $k > = 38$), MNI-coordinates in mm (BA = Brodmann area).

| Brain region | Cluster size | T | Z-score | x | y | z |
|---|--------------|-------|---------|-----|-----|-----|
| Left precentral gyrus (BA6) | 504 | 5.902 | 4.347 | -26 | -16 | 70 |
| Right precentral gyrus (BA6) | 172 | 4.624 | 3.706 | 16 | 2 | 50 |
| Right precentral gyrus (BA4) | 226 | 5.439 | 4.130 | 48 | -10 | 48 |
| Right thalamus | 130 | 5.657 | 4.234 | 16 | -20 | -4 |
| Right lentiform nucleus (globus pallidus) | 114 | 5.007 | 3.912 | 12 | 0 | 4 |
| Left cerebellum | 66 | 4.799 | 3.802 | -28 | -62 | -22 |
| Right cerebellum | 211 | 4.515 | 3.645 | 30 | -42 | -22 |
| Right cerebellum | 56 | 4.212 | 3.468 | 30 | -60 | -24 |
| Right insula | 97 | 4.384 | 3.569 | 34 | -18 | 2 |
| Right postcentral gyrus (BA3) | 66 | 4.373 | 3.563 | 38 | -44 | 64 |
| Right postcentral gyrus (BA5) | 45 | 4.230 | 3.479 | 20 | -34 | 62 |
| Right posterior cingulate | 43 | 4.263 | 3.498 | 16 | -34 | 38 |

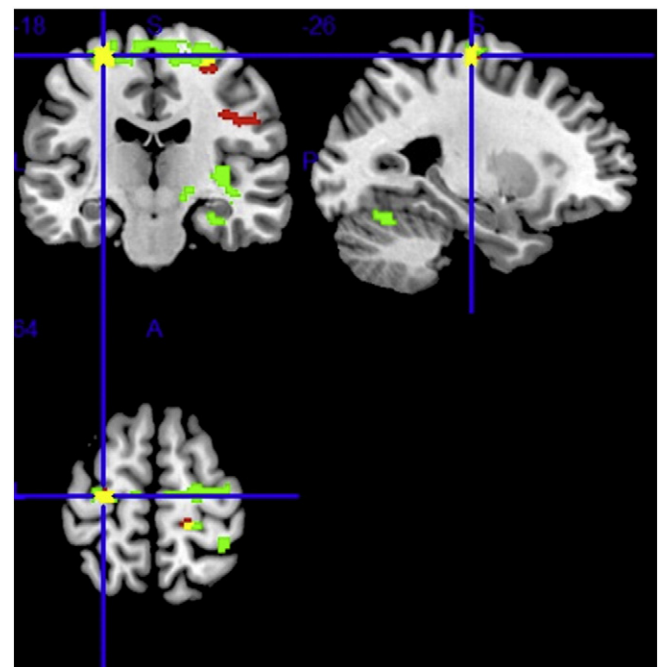


Fig. 6. Overlap between binary masks in left precentral gyrus (accuracy = green; EQ = red; overlap = yellow). Though the right hemisphere shows some yellow, which indicates overlap, these regions were not found in the SPM analyses, and are therefore not considered to be significant.

in any contrast, is considered to be part of the “classic” mirror neuron system, it has been recently suggested that this area is not as important to shared affect as the premotor cortex and inferior parietal lobe (Decety, 2011; Makuuchi, 2005; Molenberghs et al., 2009).

The significant overlap between accuracy and EQ correlations in the left premotor cortex implicates this area particularly as mediating the relationship between accuracy on the behavioural task and EQ. The function of this brain area is therefore of special interest. Activity in this task is unlikely to be directly associated with action preparation since the area that we identified was high up in the premotor cortex. Action execution studies indicate a somatotopic organisation in the premotor cortex, whereby facial actions are associated with a much more inferior area than was activated here (e.g. Buccino et al., 2001). In a review of studies of premotor cortex function, Schubotz and Von Cramon (2003) found this superior aspect of the premotor cortex to be associated specifically with tasks involving motor imagery. This includes imagery during mental rotation (de Lange et al., 2006; Ruby and Decety, 2001), when preparing to grip a bar in a variety of positions (Johnson et al., 2002), imagining foot movements (Lafleur et al., 2002) or performing actions in 1st or 3rd person (Ruby and Decety, 2001). In one of these studies, de Lange et al. (2006) found that activity in the premotor cortex and intraparietal sulcus increased with complexity on the mental rotation task. Although not measuring empathy directly, Carr et al. (2003) found robust premotor cortex activation in response to facial emotion stimuli during action observation. They suggest that the role of this area is to relate the action coding to the underlying emotional state with which it is associated and which it conveys in expression. Finally, Hooker et al. (2008) demonstrated a relationship between the premotor cortex and empathy with mental imagery tasks, correlating empathy scores to recognition of true belief over false belief stories and to making emotional inferences.

The mental imagery studies taken together with the findings reported here provide evidence for the hypothesis that the capacity to imagine action, the ability to imitate facial actions accurately and the capacity for empathy share some common neural substrates. While the insula and somatosensory cortex are thought to serve the function of representing and modulating emotion-related actions (Damasio and Carvalho, 2013), the simulation model of empathy would suggest that imitation, empathy and imagery also involve the formation of intentions. This implies that both empathy and imitation rely on forming a motor plan that corresponds to primary representations of emotions encoded in sensorimotor systems. While this may not always be necessary for the function of emotional contagion, as discussed in the introduction, it seems likely to be required for empathy under a broader definition, as described by the EQ questionnaire, which hinges on an understanding of others for interpreting the wide range of complex and ambiguous expressions of emotion that people make on a day-to-day basis. Our findings therefore provide empirical support for an important role of motor simulation in the development of empathic traits, and by extension for embodied theories of cognition (Barsalou, 2008; Niedenthal, 2007).

Some studies have argued that empathic traits are associated with emotion recognition ability. The evidence is mixed and mainly stems from the ‘mind in the eyes’ task which is also a test of emotional vocabulary (Besel and Yuille, 2010; Chapman et al., 2006). We did not find any relationship between EQ and activity in either visual processing areas or the amygdala. However, we did find a correlation between EQ and activity in somatosensory cortex, and given the potential role of action coding systems in the perception of social stimuli (Knoblich and Sebanz, 2006), this could possibly account for the relationship between EQ and emotion recognition that has been reported. In addition, the specific correlation between Imitate-versus-Mismatch and EQ in the somatosensory cortex, premotor cortex and the intraparietal sulcus implies a role for the mirror neuron system that goes well beyond action processing.

Limitations

Our study relied on a single questionnaire-based self-report measure of trait empathy. Whilst this had the advantage of specifying a single hypothesis and stemmed from previous empirical finding, it also reduces the scope for generalising these findings to other definitions and measures of empathy. In particular, we relate mirror neuron functioning to empathic behavioural traits as opposed to a direct measure of empathic functioning, such as a neurophysiologically measured emotional response. Further research will be required to determine what other measures of empathic traits or empathic functioning are associated with facial imitation ability and whether or not these are mediated by mirror neuron activity. Another consideration is that our conditions appeared to place unbalanced demands upon executive function. This is arguably inevitable if imitation, rather than contingent responding, is the default response for facial actions. Nevertheless, future designs could reduce these demands, perhaps by exploring delayed imitation, where actions are executed after the image has disappeared from the screen. Finally, we did not identify any sex effects in our sample, but we had only 10 participants for each gender. Larger studies may identify such effects.

Conclusion

In this study we sought to investigate the neural mechanisms mediating a relationship demonstrated behaviourally between facial imitation ability and empathy by investigating the brain areas involved in imitation of novel complex facial stimuli and how this activity correlates with empathy and imitative accuracy. Subtle differences between stimuli ensured that the imitation task was demanding. In addition, our control ‘mismatch’ condition appeared to elicit strong mimicry effects which required inhibition. The difference between mismatching and matching was strongly associated with activity in the bilateral insula, and insula activity also predicted task accuracy. In contrast, activity in the mirror system during imitation correlated specifically with the Empathy Quotient. In particular, an area of the premotor cortex connected in previous studies to motor imagery was associated with both the Empathy Quotient and imitation accuracy. We suggest that a motor simulation function (as opposed to the effects of mimicry) mediates the relationship between empathic behaviours (as measured by the EQ) and imitation accuracy, and that motor simulation plays an important role in the development and maintenance of these empathic behaviours. In addition, the insula is likely to be important in learning facial expressions, with imitation accuracy being determined by one's sensitivity to error feedback.

Supplementary data to this article can be found online at <http://dx.doi.org/10.1016/j.neuroimage.2013.08.061>.

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