

Right frontal cortical lesions disrupt anger mimicry

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ABSTRACT

The current study investigates the neural substrates of facial expression mimicry by assessing individuals with right and left lateralised frontal cortical lesions. Electromyography was used to measure spontaneous changes in electrical activity over the *corrugator supercilii* (brow) and *zygomaticus major* (cheek) muscle regions in response to happy and angry facial expressions. Individuals with right ($n=4$) and left ($n=5$) frontal cortical lesions and demographically matched controls ($n=9$) were compared. It was shown that while all three groups mimic happy facial expressions, only controls and individuals with left frontal lesions mimic angry expressions. These data are consistent with evidence for right frontal cortical specialisation for the processing of anger.

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1. Introduction

Viewing a facial expression spontaneously induces a congruent facial reaction in the observer (Dimberg, 1982; Dimberg & Lundquist, 1988), even when the observed face is not perceived consciously (Bailey & Henry, 2009; Dimberg, Thunberg, & Elmehed, 2000). Most investigations of the human neural substrates of this mimicry phenomenon have focused on the imitation of hand and finger movements, and only a handful have assessed facial expression mimicry. The first of these studies found that explicit instructions to imitate facial expressions result in predominantly right lateralised inferior frontal gyrus activation (Lee, Josephs, Dolan, & Critchley, 2006). However, it is of particular interest to understand the neural mechanisms of *spontaneous*, as opposed to intentional, facial expression mimicry since it has been suggested that this type of behaviour facilitates successful social interaction, including interpersonal rapport (Lakin & Chartrand, 2003) and emotion recognition (Goldman & Sripada, 2005; Oberman, Winkelman, & Ramachandran, 2007). Some studies do not find that this type of mimicry is associated with emotion recognition (Bogart & Matsumoto, 2010), but they do show that it facilitates

congruent emotions between interaction partners (Blairy, Herrera, & Hess, 1999).

Each of these potential functions of spontaneous facial expression mimicry is consistent with a motor theory of empathy (Leslie, Johnson-Frey, & Grafton, 2004). According to this theory, perceiving another's facial emotion spontaneously activates one's own motor representation of that emotion, which in turn facilitates recognition of, and empathy for, the observed emotion (Lipps, 1903; Preston & de Waal, 2002). This form of motor mimetic responding is also considered a form of empathy in its own right (Blair, 2005), with studies showing that stronger facial expression mimicry is associated with higher levels of empathy (Dimberg, Andreasson, & Thunberg, 2011; Sonny-Borgstrom, 2002), in particular when mimicry occurs via the *corrugator* (i.e., brow) region in the upper half of the face (Harrison, Morgan, & Critchley, 2010). Disruptions of mimicry in groups with reduced capacity for empathising, such as autism (McIntosh, Reichmann-Decker, Winkelman, & Wilbarger, 2006) and schizophrenia (Varcin, Bailey, & Henry, 2010) provides further evidence for the link between mimicry and empathy.

In a brain imaging study, Leslie et al. (2004) found that whereas passive viewing of a facial expression activates the right frontal cortex, explicit instructions to imitate results in bilateral frontal activation. This suggests dissociation between conscious left frontal control of facial musculature and right frontal involvement in spontaneous empathic mimicry. It has also been shown that observation of facial expression stimuli activates the right premotor cortex (Carr, Iacoboni, Dubeau, Mazziotta, & Lenzi, 2003), contributing to the suggestion that the right, but not left, frontal region may play an

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Table 1
Individual patient characteristics.

Patient	Age/sex	Localisation	Pathology	Years post surgery/(diagnosis)	GDS	NART
ME	62/F	R frontal	Meningioma	3	0	122
CJ	61/F	R frontal	Meningioma	13	8	100
DB	45/M	R posterior frontal	AVM	7	14	98
KM	62/M	R posterior frontal	AVM	(3)	18	111
DE	75/F	L frontal	AVM	6	2	91
LH	56/F	L frontal	Cavernous malformation	(5)	5	102
VS	49/F	L frontal	Meningioma	(7)	15	–
DC	68/F	L frontal	Meningioma	2	6	107
SP	54/F	L frontal	Unspecified autoimmune	2	4	112

AVM = arteriovenous malformation; GDS = Geriatric Depression Scale score; NART = National Adult Reading Test Full Scale IQ; F = female; L = left; M = male; R = right.

important role in spontaneous facial expression mimicry. The only other study to assess the neural substrates of spontaneous facial expression mimicry suggests that the frontal regions may be particularly important for the mimicry of angry, but not happy, facial expressions. Specifically, individuals with traumatic brain injury did not mimic angry facial expressions, and this was attributed to the involvement of ventral frontal damage in this type of injury (McDonald et al., 2011).

However, there have been no lesion studies to date that have specifically investigated the role of the right frontal cortex in facial expression mimicry, which clearly seems an important next step in delineating the neural substrates of this behaviour. Indeed, Dimberg and Petterson (2000) show that mimicry of angry and happy facial expressions produces stronger muscle activity on the left than the right side of the face, suggesting right hemisphere dominance in imitative behaviour. In addition, individuals with injury to the right hemisphere are less able to produce positive and negative facial expressions (Borod, Koff, Lorch, & Nicholas, 1985; Borod, Koff, Lorch, & Nicholas, 1986), and have difficulty recognising basic emotional expressions (Adolphs, Damasio, Tranel, & Damasio, 1996). Further evidence for the potential importance of the right hemisphere in processing facial expressions comes from a study showing improved recognition of emotional valence when expressions are presented to the left rather than the right visual field (Natale, Gur, & Gur, 1983).

More specifically, it has been shown that a patient with focal right frontal trauma demonstrated impairment in recognition of, and autonomic responding to, angry expressions, as well as high levels of aggressive behaviour and difficulty understanding others' anger (Blair & Cipolotti, 2000). Together with evidence that viewing angry facial expressions activates the right orbitofrontal cortex (Blair, Morris, Frith, Perrett, & Dolan, 1999), it has been suggested that the right frontal region represents a specialised system for responding to, and generating expectations of, others' anger (Blair & Cipolotti, 2000). In contrast, activations in non-frontal regions have been associated with smiling to happy expressions (Lee et al., 2006), as well as with viewing happy faces (Phan, Wager, Taylor, & Liberzon, 2002). A further study shows that processing negative expressions results in greater orbitofrontal activity relative to happy expressions (Iidaka et al., 2001). These studies suggest that damage to the right frontal region may disrupt the mimicry of angry, but not happy, facial expressions.

Spontaneous facial mimicry responses are generally detected in experimental settings using facial electromyography (EMG; measurement of changes in the electrical activity of muscles), which is sensitive to even subtle changes in facial muscle activity. Numerous EMG studies have shown that images of angry facial expressions evoke increased *corrugator supercilii* (i.e., brow) activity relative to images of other types of expressions. In addition, happy facial expressions elicit greater *zygomaticus major* (i.e., cheek) activity relative to other types of expressions. Using this technique, the present

study was the first to assess spontaneous facial expression mimicry among individuals with lesions localised to either the right or left frontal cortex. It was predicted that right frontal cortical lesions would disrupt the spontaneous mimicry of angry, but not happy, facial expressions.

2. Method

2.1. Participants

Five adults with lesions localised to the left frontal cortex (5 female), and four with lesions localised to the right frontal cortex (2 female, 2 male), participated in the current study. Patient information is given in Table 1. All were recruited from the Prince of Wales Hospital, Sydney, based on clinical reports from neurosurgeons at the hospital. Only patients whose medical records indicated no prior neurological or psychiatric disorders and no evidence of aphasia or agnosia, and were deemed by treating clinical staff to have sufficient cognitive capacity to understand and comply with instructions were recruited. The experimenter also independently determined throughout testing that all had sufficient cognitive and motor capacity to understand and comply with instructions. Nine demographically matched controls (7 female) also participated in the current study. Exclusion criteria for all control participants included a self-reported psychological or neurological disorder, alcohol/drug abuse and experimenter-determined inability to communicate adequately. All participants received \$10 Australian (~10 USD) per hour for participation. Patients and controls did not differ in age ($M = 59.1$ years, $SD = 9.28$; $M = 59.4$ years, $SD = 9.65$, respectively; $t(16) = .08$, $p = .94$, $d = .03$), years of education ($M = 13.0$ years, $SD = 3.20$; $M = 13.7$ years, $SD = 2.60$, respectively; $t(16) = .49$, $p = .63$, $d = .24$), or premorbid intelligence as measured by Full Scale IQ on the National Adult Reading Test (Nelson & Willison, 1991; $M = 105.4$, $SD = 9.68$; $M = 110.3$, $SD = 9.80$, respectively; $t(15) = 1.05$, $p = .31$, $d = .50$). Note that one patient did not complete the NART since English was their second language. In addition, there was a non-significant trend for depression scores to be higher for patients ($M = 8.0$, $SD = 6.27$) than controls ($M = 4.1$, $SD = 4.14$; $t(16) = 1.55$, $p = .14$, $d = .73$), as measured by the 30-item Geriatric Depression Scale (Yesavage et al., 1983). Importantly, however, no participants scored within the severely depressed range on this scale (i.e., 20–30), and only four scored within the mildly depressed range (i.e., 10–19; see Table 1 for individual depression and NART scores). All participants provided informed consent according to the Declaration of Helsinki. Ethics approval for this study was obtained from the South-Eastern Sydney Illawarra Area Health Service – Eastern Section and the University of New South Wales ethics committee.

2.2. Passive viewing paradigm

Surface EMG was used to record changes in the level of muscle activity over the left *corrugator supercilii* region, which knits the brow, and the left *zygomaticus major*, which lifts the corners of the lips into a smile. Site preparation and electrode placement followed the standard procedure set out by Tassinari and Cacioppo (2000). The skin over the regions of interest was cleansed with an alcohol wipe and then gently abraded with NuPrep gel. The electrodes were gold-plated, hat-shaped discs with 9 mm housings that were placed in pairs, with an inter-electrode distance of approximately 1.25 cm, and with an additional electrode approximately in the centre of the forehead acting as an earth. The electrodes were attached with Ten20 conductive paste. Muscle activity was continuously recorded with a PowerLab 4/30 Data Acquisition System (AD Instruments, Castle Hill, Australia) at a sampling rate of 2000 Hz with a 10–500 Hz bandpass filter, a 50 Hz notch filter, and an amplification factor of 20,000. The PowerLab was triggered by DMDX (Version 3.2.3.0; Forster & Forster, 2003), which synchronised timing of the facial expression presentations with the recording of the data acquisition system.

Participants were asked to sit in a comfortable chair and watch a series of stimuli on a monitor. To disguise the true purpose of the study participants were also told that the EMG sensors were measuring changes in the sweat gland activity of their

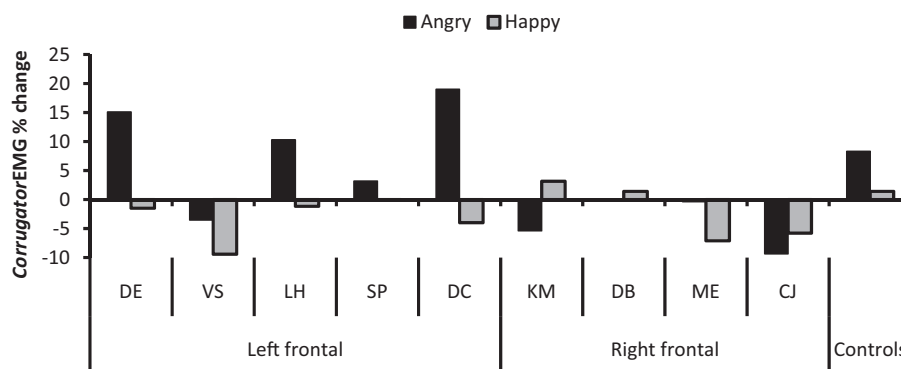


Fig. 1. Average percentage change in *corrugator* activity within 1 s of stimulus exposure for individuals with left and right frontal lesions, and control participants. Controls Angry SE = 2.43, Happy SE = 1.42.

skin (see Dimberg & Thunberg, 1998). The stimuli were 16 × 24 cm black and white pictures of happy and angry facial expressions (Ekman & Friesen, 1975) that were presented approximately 60 cm in front of the participant. Each trial commenced with a 50 ms soft orienting tone which was followed by the presentation of a facial expression 1 s later. Each face was displayed on the monitor for 4.5 s, followed by a blank screen for 6 s. Pictures of eight different people (4 male, 4 female), but all with the same expression, were presented in a block which was randomised using DMDX. Each participant viewed a total of two blocks (1 happy, 1 angry), and these blocks were counterbalanced across participants.

Raw EMG signals were screened for electrical noise and movement artefacts. In addition, a coder who was blind to condition watched videotapes of each participant and noted when they were not watching the stimulus or when they made extraneous movements such as yawning. These amounted to <5% of trials, which were deleted from subsequent analyses. It should also be noted that an orienting tone, rather than a fixation cross, was particularly suitable for the current procedure because it not only alerted the participant to the presentation of the stimulus, but it also indicated the later time at which they should expect the participant to be looking at the monitor.

The average EMG signal was calculated using the root-mean-square (RMS) method, which represents the square root of the average power of the EMG signal over a given period of time (Tassinari & Cacioppo, 2000). The baseline for each trial was calculated as the average RMS EMG activity .5 s prior to each stimulus presentation. Potential variability of responses across trials was reduced by calculating the average of each 100 ms window separately for each expression valence (8 happy, 8 angry). Subsequently, the average RMS EMG percentage change from baseline (normalised EMG), averaged across individual trials within each block, was calculated separately for the windows from 0 to 1 s (rapid timeframe) and from 0 to 4.5 s (entire duration) post stimulus onset, consistent with McDonald et al. (2011).

3. Results

3.1. Baseline activity

To test whether there were any differences in baseline muscle activity (.5 s pre-stimulus exposure), 2 × 3 analyses of variance (ANOVAs) were conducted separately for the *corrugator* and *zygomaticus* regions with the within-groups variables of emotion (happy, angry) and between-groups variables of participant group (controls, left frontal, right frontal). For the *corrugator*, there was no main effect of emotion, $F(1, 15) = 3.64$, $p = .076$, $\eta_p^2 = .195$, or group, $F(2, 15) = .42$, $p = .668$, $\eta_p^2 = .052$, and no emotion × group interaction, $F(2, 15) = 1.72$, $p = .212$, $\eta_p^2 = .187$. For the *zygomaticus*, there was no main effect of emotion, $F(1, 15) = .15$, $p = .706$, $\eta_p^2 = .010$, or group, $F(2, 15) = .48$, $p = .627$, $\eta_p^2 = .060$, and no emotion × group interaction, $F(2, 15) = 2.59$, $p = .108$, $\eta_p^2 = .256$.

3.2. Mimicry of angry facial expressions: *corrugator* activity

To ascertain whether appropriate anger mimicry was shown by each group (i.e., whether *corrugator* activity was greater in response to angry relative to happy facial expressions), 3 (group: controls, left frontal, right frontal) × 2 (expression: angry, happy) mixed-design ANOVAs were conducted separately for the rapid timeframe

(0–1 s) and the entire display duration (0–4.5 s). In the rapid timeframe, there was a main effect of emotion, $F(1, 15) = 10.86$, $p = .005$, $\eta_p^2 = .420$, indicating that across groups there was more *corrugator* activity to angry relative to happy expressions, which is indicative of a typical anger mimicry response (see Fig. 1). There was no main effect of group, $F(2, 15) = 3.33$, $p = .063$, $\eta_p^2 = .308$, but the emotion × group interaction was significant, $F(2, 15) = 4.31$, $p = .033$, $\eta_p^2 = .365$.

Further investigation of this interaction revealed a simple main effect of anger, $F(2, 15) = 4.40$, $p = .031$, $\eta_p^2 = .370$. Bonferroni post hoc *t*-tests showed that compared to those with right frontal lesions, there was more *corrugator* activity to angry expressions among individuals with left frontal lesions ($p = .021$) and controls ($p = .015$), and the latter two groups did not differ ($p = .906$). There was no simple main effect of happiness, $F(2, 15) = 1.83$, $p = .194$, $\eta_p^2 = .196$. In addition, there were simple main effects for the controls, $F(1, 15) = 8.77$, $p = .010$, $\eta_p^2 = .369$, and the individuals with left frontal lesions, $F(1, 15) = 14.82$, $p = .002$, $\eta_p^2 = .497$, but not those with right frontal lesions, $F(1, 15) = .23$, $p = .639$, $\eta_p^2 = .015$. Bonferroni post hoc *t*-tests showed there was more *corrugator* activity to angry relative to happy stimuli within 1 s of stimulus exposure among controls ($p = .010$) and individuals with left frontal lesions ($p = .002$), indicative of the typical anger mimicry response.

Across the entire duration of the display (0–4.5 s), there was no main effect of emotion, $F(1, 15) = 2.02$, $p = .176$, $\eta_p^2 = .119$, or group, $F(2, 15) = 2.41$, $p = .124$, $\eta_p^2 = .243$, but there was an emotion × group interaction, $F(2, 15) = 7.31$, $p = .006$, $\eta_p^2 = .494$. In an analysis of this interaction, tests of simple effects revealed a simple main effect of angry, $F(2, 15) = 5.89$, $p = .013$, $\eta_p^2 = .440$, but not happy stimuli, $F(2, 15) = .05$, $p = .949$, $\eta_p^2 = .007$. Bonferroni post hoc *t*-tests showed that, relative to participants with right frontal lesions, controls and left frontals responded with more *corrugator* activity to angry expressions ($p = .007$ and $p = .008$, respectively), and no difference was observed between left frontals and controls ($p = .718$).

Further tests of simple effects revealed a simple main effect of emotion within each group; controls, $F(1, 15) = 7.34$, $p = .016$, $\eta_p^2 = .328$, left frontals, $F(1, 15) = 8.01$, $p = .013$, $\eta_p^2 = .348$, and right frontals, $F(1, 15) = 4.88$, $p = .043$, $\eta_p^2 = .245$, indicating that *corrugator* activity was greater in response to angry relative to happy expressions for the control group and the individuals with left frontal lesions, consistent with a typical mimicry response. The reverse pattern was observed among the individuals with right frontal lesions (see Fig. 2).

3.3. Mimicry of happy facial expressions: *zygomaticus* activity

To ascertain whether appropriate mimicry of happy facial expressions was shown by each group (i.e. whether *zygomaticus*

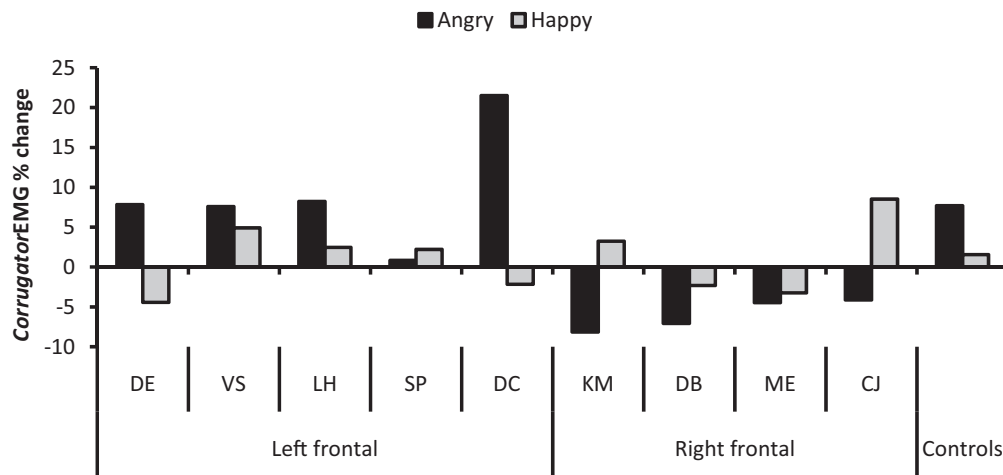


Fig. 2. Average percentage change in *corrugator* activity across the entire duration of the display (0–4.5 s) for individuals with left and right frontal lesions, and control participants. Controls Angry SE = 2.44, Happy SE = 1.87.

activity was greater in response to happy relative to angry expressions), 3 (group: controls, left frontal, right frontal) $\times$ 2 (expression: happy, angry) mixed-design ANOVAs were conducted separately for the rapid (0–1 s) and overall (0–4.5 s) timeframes. In the rapid timeframe (0–1 s), there was a main effect of emotion, $F(1, 15) = 10.22$, $p = .006$, $\eta_p^2 = .405$, indicating that across groups, there was more *zygomaticus* activity to happy than angry facial expressions, which is in line with a typical pattern of mimicry (see Fig. 3). There was no main effect of group, $F(2, 15) = 1.22$, $p = .323$, $\eta_p^2 = .140$, and no interaction between emotion and group, $F(2, 15) = .829$, $p = .455$, $\eta_p^2 = .100$.

In the overall timeframe (0–4.5 s), there was a main effect of emotion, $F(1, 15) = 19.19$, $p = .001$, $\eta_p^2 = .561$, indicating that across each group there was greater *zygomaticus* activity in response to happy relative to angry facial expressions, which is indicative of a typical mimicry response (see Fig. 4). There was no main effect of group, $F(2, 15) = 1.77$, $p = .204$, $\eta_p^2 = .191$, and no emotion $\times$ group interaction, $F(2, 15) = 2.09$, $p = .159$, $\eta_p^2 = .218$.

4. Discussion

To the present authors' knowledge, the current study was the first to assess facial expression mimicry among individuals with right and left lateralised frontal cortical lesions. Electromyography

was used to measure changes in electrical activity over the *corrugator* and *zygomaticus* muscle regions in response to passive viewing of happy and angry facial expressions. It was shown that whereas controls and individuals with left frontal lesions spontaneously mimic angry facial expressions, individuals with right frontal lesions do not, with this effect evident within 1 s of stimulus exposure, and across the entire duration of the display. It was also shown that all three groups spontaneously mimic happy facial expressions, both rapidly (i.e., within 1 s of stimulus exposure) and across more extended durations (i.e., the entire 4.5 s duration of the display). These data are consistent with studies suggesting a specialised right frontal region for responding to, and generating expectations of, others' anger (Blair et al., 1999; Blair & Cipolotti, 2000), and extend this specialisation to the *mimicry* of angry facial expressions. Given that mimicry is considered to be a low-level precursor to empathic responding (Blair, 2005; Lipps, 1903; Preston & de Waal, 2002), our data suggest that disrupted processing of others' anger in the context of right frontal damage may be at least partly attributable to impaired anger mimicry.

These data are consistent with other studies showing selective disruption of angry facial expression mimicry in patient groups (e.g., McDonald et al., 2011). The findings also suggest that the bilateral frontal cortex might not be important for the mimicry of happy expressions, although this interpretation is qualified by the possibility that the lesions of the participants in the current

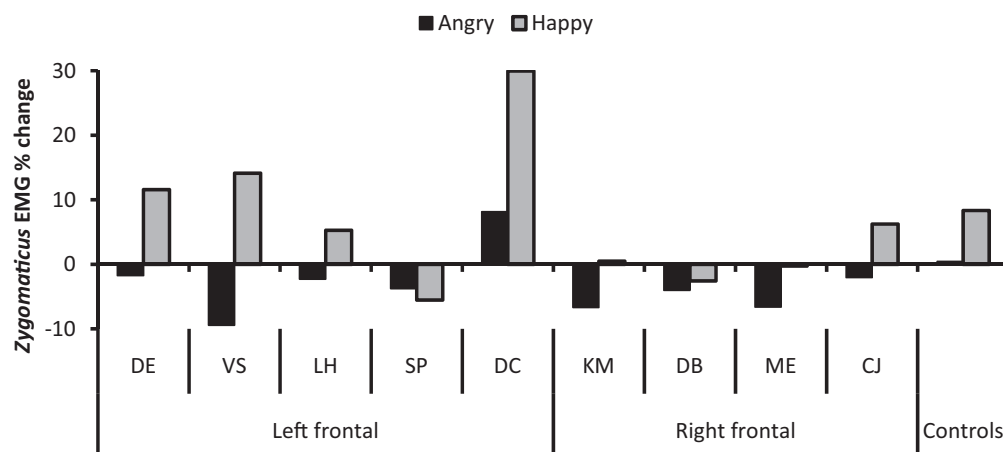


Fig. 3. Average percentage change in *zygomaticus* activity within 1 s of stimulus exposure for individuals with left and right frontal lesions, and control participants. Controls Angry SE = 1.83, Happy SE = 3.53.

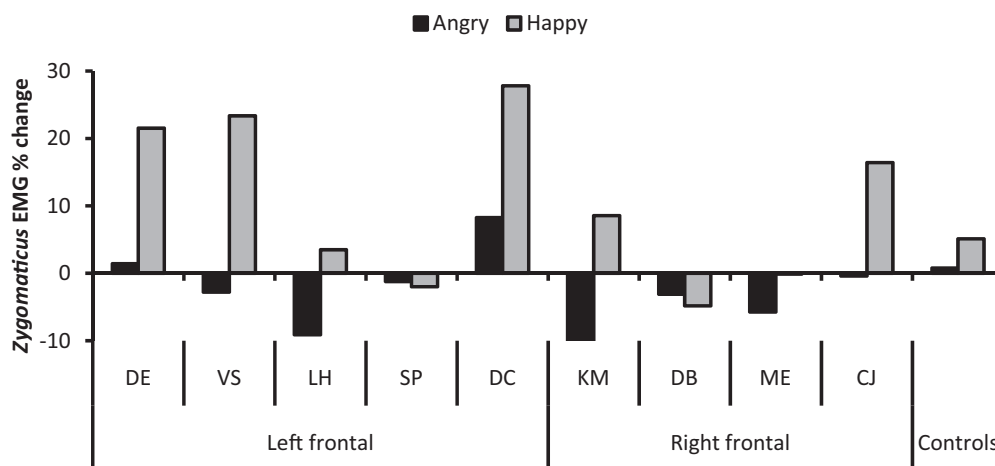


Fig. 4. Average percentage change in zygomaticus activity across the entire duration of the display (0–4.5 s) for individuals with left and right frontal lesions, and control participants. Controls Angry $SE = 2.16$, Happy $SE = 3.25$.

study may not have overlapped with the specific frontal structures essential for this type of mimicry. Indeed, the nature of data collection was a limitation of the current study in terms of the lack of precise information about lesion locations within the broader right and left frontal regions. Nevertheless, it can be seen that whether the mimicry of happy expressions relies on frontal regions or not, these data provide strong evidence that at least some of the neural substrates essential for this type of mimicry are distinct from those essential for anger mimicry.

As noted previously, mimicry of facial expressions produces stronger muscle activity on the left than on the right side of the face, and conventional EMG guidelines therefore recommend taking measurements from the left side of the face to optimise sensitivity to changes in facial musculature (Tassinari & Cacioppo, 2000). It might be suggested that findings were biased against individuals with right frontal lesions because if they were relying on their intact left frontal brain for mimicry, this would presumably result in stronger muscle activity on the right side of the face. However, these individuals were shown to mimic happy expressions, suggesting that electrode placement was sufficient to capture facial responding. Moreover, contralateral innervation does not specify activity exclusively on one side of the face, but rather moreso on one side than the other (Dimberg & Petterson, 2000). This in turn suggests that if anger mimicry was intact among those with right frontal lesions the appropriate muscle activity would have been seen on both sides of the face, albeit moreso on the right. As noted above, the lack of evidence in the current study for left frontal control over the mimicry of angry facial expressions is also consistent with previous research (e.g., Blair & Cipolotti, 2000; Blair et al., 1999).

In the current study, right frontal lesions resulted in relaxation of the *corrugator* muscle region in response to expressions of anger. This type of responding (previously described as counter mimicry) may represent difficulties with affective regulation as relaxation of the *corrugator* typically occurs in response to positive stimuli (Likowski, Muhlberger, Seibt, Pauli, & Weyers, 2011). Therefore, when this behaviour is seen in response to another's anger, it may be associated with *schadenfreude*, or the derivation of pleasure from the disadvantage of a competitor (Likowski et al., 2011). Similarly, observing another's anger is believed to elicit behavioural extinction or response reversal that acts to suppress the observer's current behaviour (Blair et al., 1999). Thus, the relaxation of the brow in response to anger in the current study may represent a failure to reverse or suppress a positive affective state when presented with an angry expression. A further alternative explanation for the relaxation of the *corrugator* is that these individuals raised

their eyebrows in either surprise or fear. This would indicate that although individuals with right frontal lesions do not mimic angry faces, they remain reactive to them. Further studies are needed to delineate the mechanisms underpinning this relaxation of the *corrugator* in response to anger among individuals with injury to the right frontal cortex.

There are some potential limitations to the current data that remain to be addressed. First, it is important to note that happy and angry expressions differ not only in their basic emotion category, but also in terms of positive versus negative emotional valence. We therefore cannot rule out the possibility that right frontal cortical specialisation for anger mimicry might also reflect specialisation for mimicry of negative facial expressions in general, including, for example, anger, sadness, and fear. Interestingly, while each of these negative emotions activates the brow region of the upper face, happiness and smiling instead primarily innervate lower facial regions. As such, the current data may also reflect the importance of the right frontal cortex for mimicry of emotions that specifically innervate muscles in the upper regions of the face.

Impaired upper face mimetic responding may in turn reflect empathic deficits among patients with right frontal lesions. This hypothesis is consistent with evidence that mimicry in the upper face *corrugator*, but not lower face *zygomaticus*, is associated with empathy (de Wied, van Boxtel, Zaalberg, Goudena, & Matthys, 2006; Harrison et al., 2010; Hermans, van Wingen, Bos, Putman, & van Honk, 2009). The importance of the upper face in empathic mimetic responding highlights a potential link between the proposed neural anatomy of facial emotional expressions (Morecraft, Louie, Herrick, & Stilwell-Morecraft, 2001) and how this anatomical circuitry may be implicated in empathic mimicry (Morecraft et al., 2007; Harrison et al., 2010). Emotion perception activates lateral and basal amygdala nuclei, but whereas cingulate motor cortices representing the upper face have strong bidirectional connectivity with the basal amygdala, those representing the lower face are only weakly connected with this region. As pointed out by Harrison et al. (2010), the basolateral amygdala in turn is strongly connected to regions mediating emotional responses, which suggests that upper face mimicry may provide the more direct representation of amygdala responses.

It might be argued that the current data simply reflect angry expressions being more difficult to mimic than happy expressions, but there is some evidence to suggest that this is not the case. First, both angry and happy expressions are mimicked subconsciously and rapidly, suggesting that although happy expressions are often recognised and labelled more easily than other expressions

(Ruffman, Henry, Livingstone, & Phillips, 2008), they may not necessarily be mimicked more easily. Second, the *corrugator* is more differentially responsive to positive versus negative affect than other facial muscle regions, including the *zygomaticus* (Cacioppo, Bush, & Tassinari, 1992). This indicates that mimicking a happy expression might be more difficult than mimicking an angry one. A final limitation of the current study may be that including males in the right, but not left, frontal lesion sample could explain the poorer mimicry among right frontals. This is because females typically find it easier than males to recognise emotions (Hall, Carter, & Horgan, 2000), and to experience empathy (e.g., Baron-Cohen & Wheelwright, 2004). However, this potential limitation may be minimal considering that right frontal patients only showed difficulty mimicking angry, and not happy, expressions. In addition, some studies find that males and females do not differ in the recognition of facial expressions, including anger (e.g., Grimshaw, Bulman-Fleming, & Ngo, 2004).

In conclusion, the present study represents an important step in directly identifying the neural regions of interest in spontaneous facial expression mimicry. The data in particular highlight a dissociation in the neural substrates implicated in spontaneous responses to happy and angry facial expressions, and also complement other evidence attributing a particularly important role to the right frontal cortex in anger mimicry specifically. Future studies are now needed to more precisely delineate the specific regions within the right frontal cortex that are responsible for anger mimicry, as well as to identify the neural substrates responsible for the mimicry of happy facial expressions.

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