



Research Report

Pre-SMA activation and the perception of contagiousness and authenticity in laughter sounds



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ABSTRACT

Functional near-infrared spectroscopy and behavioural methods were used to examine the neural basis of the behavioural contagion and authenticity of laughter. We demonstrate that the processing of laughter sounds recruits networks previously shown to be related to empathy and auditory-motor mirror networks. Additionally, we found that the differences in the levels of activation in response to volitional and spontaneous laughter could predict an individual's perception of how contagious they found the laughter to be.

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1. Introduction

Laughter is a very simple sound to produce and it is one of the earliest vocalisations that babies make (Addyman & Addyman, 2013; Scott et al., 2014). However, adults use laughter in a myriad of ways to convey meaning and express emotion in conversational interactions (Mazzocconi et al., 2020). Within a given social interaction, a listener needs to be able to judge the authenticity, as well as the emotional relevance, of those sounds. The ability to generate appropriate

responses to non-verbal cues is essential for communication and is an important aspect of *social cognition* (Shettleworth, 2001). For example, one person laughing hysterically during a conversation while the other person merely chuckles can create an awkward situation that might even be considered offensive.

Laughter is an overwhelmingly social phenomenon; an individual is up to 30 times more likely to laugh when with others than when alone (Provine & Fischer, 1989). Laughter is a highly contagious behaviour: one of the most effective triggers

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of laughter is another person's laughter (Hatfield et al., 1993; Hietanen et al., 1998; Mazzocconi et al., 2020; O'Nions et al., 2017; Provine, 1992; Wild et al., 2003). Due to laughter's high levels of contagion, laugh tracks, or “canned laughter” have been used on television since the 1950's to compensate for having a large audience (Provine, 2016, p. 201). The simple presence of laughter can make a joke seem funnier, and this effect is even more significant if the laughter heard was spontaneous (Cai et al., 2019).

Due to its level of importance in social behaviour, numerous philosophers such as Plato, Aristotle, Descartes, Hobbes, Kant, Darwin, and Freud have tried to understand why laughter happens and what it signifies (Morreall, 1987). Several studies have mapped out aspects of the neural areas recruited during the perception of laughter, indicating the prefrontal cortex, primary motor cortex, somatosensory cortex, pre-supplementary motor area (pre-SMA), supplementary motor area (SMA), inferior frontal gyrus (IFG), anterior insula (AI), superior and middle temporal lobes (STS/STG), paracentral lobule, hippocampus, amygdala, inferior parietal lobe (IPL), anterior cingulate cortex (ACC), and temporal poles (Agnew et al., 2017; Lavan & McGettigan, 2017; McGettigan et al., 2015; O'Nions et al., 2017; Szameitat et al., 2010; Warren et al., 2006; Wild et al., 2003).

There are two distinct neural systems underlying human vocalisations. The production of spontaneous vocalisations (e.g., involuntary emotional vocalisations) relies upon the midline neuronal system, including the PAG, ACC, and pre-SMA, while intentional sounds (e.g., speech, communicative laughter) engage the lateral premotor and motor areas, as well as the SMA, cerebellum and basal ganglia (Jürgens, 2002; Scott et al., 2014). Consistent with the differences in production, volitional and spontaneous laughter types exhibit different acoustic and phonetic properties (Lavan et al., 2016). Laughter sounds that contain more voiced components are rated as increasingly volitional, possibly because they sound more similar to language (Bryant & Aktipis, 2014). Volitional laughter is not necessarily “fake laughter”, with the aim to deceive, but it can signal different meanings in different contexts (Mazzocconi et al., 2020). It can also be used to engage the listener's interest and attention, and is often used at the end of sentences, almost like a full stop (Chapman & Wright, 1976; Provine, 2016, p. 200).

The orofacial mirror network supports the automatic impulse to respond to behaviourally contagious emotions, and comprises the pre-SMA, SMA, sensorimotor cortices, IFG, IPL, superior temporal lobes, ACC and AI (Kohler et al., 2002; Lima et al., 2015, 2016; McGettigan et al., 2015; Warren et al., 2006). Spontaneous laughter is rated as being more authentic, contagious, and signalling higher valence intensity and behavioural arousal relative to volitional laughter (McGettigan et al., 2015). People automatically try to understand heard laughter, arguably because it is always socially meaningful (McGettigan et al., 2015). The ability to correctly judge the level of authenticity of an emotional vocalisation varies from person to person, and these individual differences relate to the increased engagement of parts of the affective sharing network (McGettigan et al., 2015).

The aim of this study was to determine the pattern of cortical activity that predicts an individual's conscious

perception of the level of contagiousness of laughter sounds. We hypothesized that the activation of the premotor and motor areas would be related to levels of contagion and authenticity due to the role of these regions in auditory-motor integration and motor priming (Lima et al., 2015, 2016; McGettigan et al., 2015; Wattendorf et al., 2016).

2. Data collection

We report how we determined our sample size, all data exclusions (if any), all inclusion/exclusion criteria, whether inclusion/exclusion criteria were established prior to data analysis, all manipulations, and all measures in the study.

2.1. fNIRS testing

Functional magnetic resonance imaging (fMRI) and functional near-infrared spectroscopy (fNIRS) measure the same physiological phenomenon: as neuronal activity intensifies in response to a stimulus, the local cerebral vasculature enables a rise in cerebral blood flow that results in a localized increase in the concentration of oxyhemoglobin (HbO) and decrease in the concentration of deoxyhemoglobin (HbR). fNIRS relies on the fact that HbO and HbR exhibit distinct absorption spectra in the near-infrared wavelength range. The relative changes in the detected intensity of NIR light is dependent on the cerebral concentration of hemoglobin species. The measured changes in intensity can only occur in a given neuroanatomical region within the cortex that underlies an fNIRS channel, and multiple fNIRS channels can be combined to provide significant spatial information.

To examine the neurological correlates of the response to laughter sounds, the changes in hemoglobin concentration were obtained from a 52-channel fNIRS system that simultaneously emits light at 695 nm and 830 nm wavelengths (Hitachi ETG 4000). The array consisted of 17 source and 16 detector positions, forming 52 channels. The bilateral probe was placed over the frontal, central and temporal regions of the brain in accordance with the international 10/20 system, shown in Fig. 1. To ensure consistent spatial sampling and to allow for cortical registration, subject-specific anatomical and optode positioning data were collected with the Polhemus Patriot Digitizer (Polhemus, Colchester, Vermont). These 3D positions were used within the software package AtlasViewer (Aasted et al., 2015) to quantify the measurable sensitivity of each channel to the cerebral cortex, and then determine associated cortical labels. The Monte-Carlo derived forward model was used to model the sensitivity of each channel (Aasted et al., 2015; Fang & Boas, 2009).

Fourteen participants took part in the study, including eight males and six females. The fNIRS acquisition paradigm used the same laughter clips as used for the behavioural testing, but grouped the clips by laughter type to create 16-s-long blocks more suitable for fNIRS measurements (McGettigan et al., 2015). These laughter blocks alternated with a silent condition lasting approximately 12 sec. Stimuli were presented on a 24” screen using MATLAB 2017b with the Psychophysics toolbox extension (Brainard, 1997). Participants were instructed to stare at a blank computer screen and

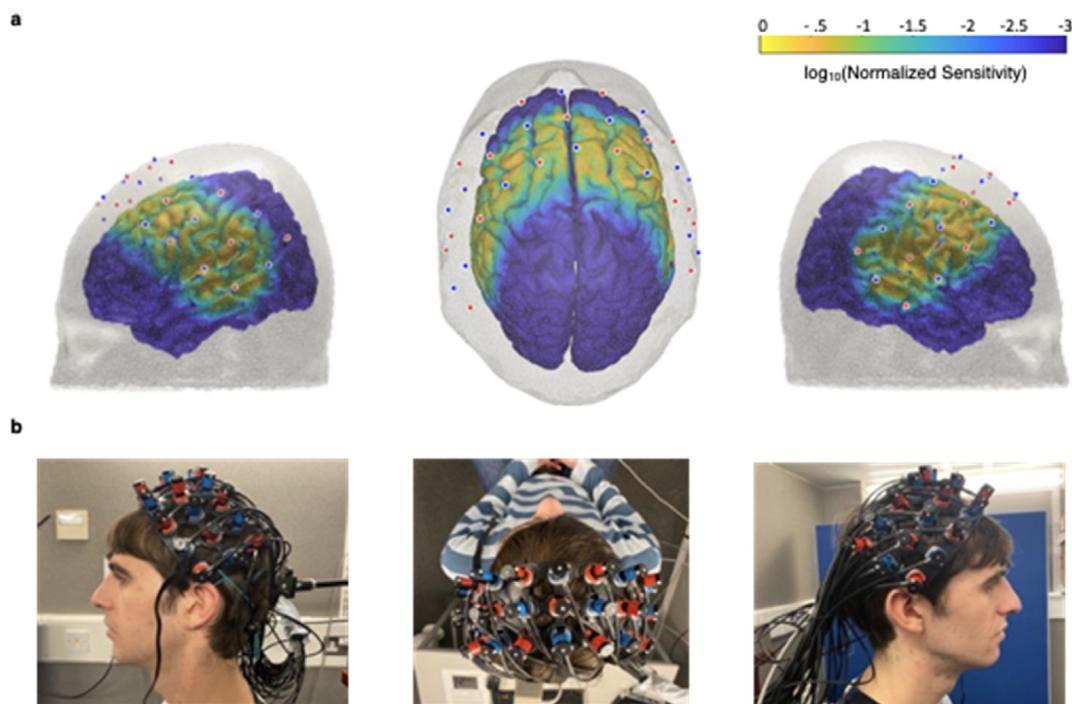


Fig. 1 – fNIRS data collection. (a) The grid array was placed on the scalp at a location designed to maximise the likelihood of recording activation, in the temporal lobes and motor areas. (b) A subject demonstrating cap placement.

focus on the sounds for the duration of the testing period, which was approximately 8 minutes long.

2.2. Behavioural testing

The purpose of this portion of the experiment was to confirm that this participant pool could detect the different laughter type's levels of authenticity and contagion that were consistent with the literature (McGettigan et al., 2015). Participants completed a post-hoc behavioural test where they listened to spontaneous and volitional laughter clips (McGettigan et al., 2015) and ranked the level of authenticity and contagiousness for each sound on a scale of 1–7, with 1 being the lowest and 7 the highest. Behavioural testing was controlled using MATLAB 2017a on a 13" MacBook Pro and custom scripts. The 19 different laughter sounds (McGettigan et al., 2015), each approximately 2 sec long, were played in a randomized order. Each sound was rated after presentation of the stimulus. These sounds have been examined for acoustic differences between spontaneous and volitional clips (Lavan & McGettigan, 2017; McGettigan et al., 2015).

3. Analysis and results

3.1. Behavioural ratings

These responses were collected post-hoc; however, they are presented first in order to have a more clear narrative. The distribution of results showed stark differences in behavioural ratings for contagion and authenticity (Fig. 2, Supplementary

Table 1). Additionally, there was a pronounced ceiling effect, which was especially evident for contagion as 70.8% of responses were a 7. A Wilcoxon signed-rank test was used, and levels of significance were corrected against multiple comparisons using the Benjamini-Hochberg procedure. Results showed that both authenticity and contagiousness ratings were significantly higher for spontaneous laughter (Authenticity $p = 6.59e^{-21}$, $Z = 9.38$; Contagion $p = 1.13e^{-28}$, $Z = 11.16$). The overview of responses are shown in Supplementary Table 1.

Next, we sought to determine whether the participants' ratings of authenticity and contagiousness of the laughter sounds were related to each other. Both types of laughter were analyzed using Spearman's correlation, which revealed a strong positive monotonic relationship ($r_s = .695$, $p < .00001$) shown in (Fig. 3). This demonstrated that a laughter sound that is deemed more contagious is also more likely to sound highly authentic.

3.2. Neural responses to volitional and spontaneous laughter

We calculated the neural responses of each laughter type compared to baseline, and if these patterns of activation were significantly different when contrasted against each other. We used two different methods to ensure that the probes were consistently positioned across subjects. We began by registering the location of each subject's optodes into MNI space (Holmes et al., 1998). To determine the level of precision in the measurements, we calculated the average Euclidian error for each channel across all subjects. This represents in 3D how

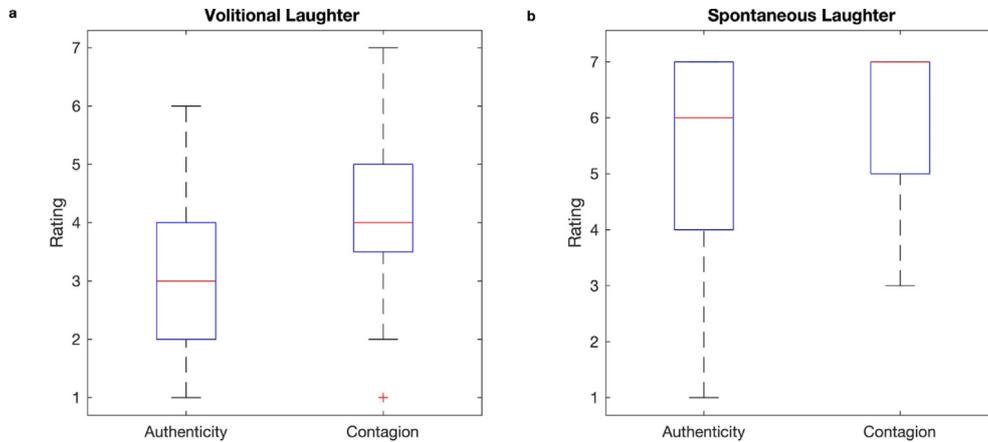


Fig. 2 – Behavioural ratings for volitional (a) and spontaneous (b) laughter. The median of the interquartile range is shown in red. This illustrates the extent to which the distribution of ratings is skewed.

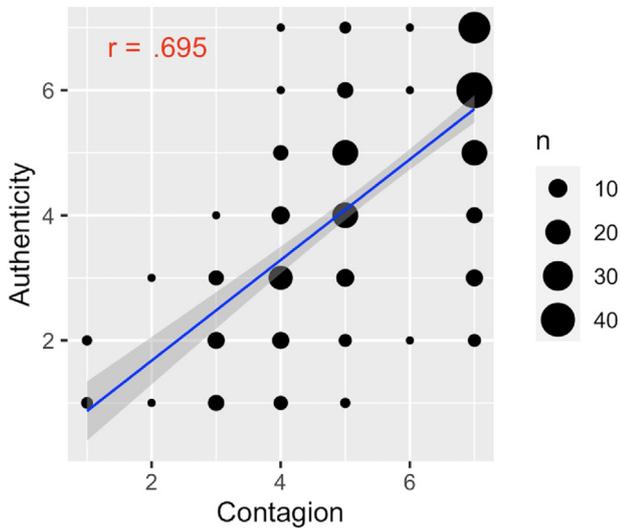


Fig. 3 – Relationship between authenticity ratings and contagiousness ratings for all laughter sounds. The distribution of the ratings are also shown.

the different location of each channel as defined by Atlas-Viewer was from the average position within the MNI space (avg = 11.9 mm; standard deviation = 5.1). To visualise this distribution across the group, the photon measurement density function (PMDF) of an example channel for every subject was projected onto the brain (Supplementary Fig. 1).

Data were analysed using the NIRS Brain AnalyZIR toolbox (Santosa et al., 2018). Raw intensity data was collected at 10 Hz, then downsampled to 4 Hz before being converted to HbO, HbR and HbT concentrations. The autoregressive pre-whitening iteratively reweighted least squares AR(P)-IRLS canonical linear model was used to determine the beta weights for each channel in response to each stimulus condition (Barker et al., 2013). By pre-whitening the channel data, the GLM statistically accounts for serially correlated physiological noise such as respiration, heart rate, and blood pressure. Instead of removing data, the robust regression works to iteratively down-weight outliers such as motion artifacts.

The vector of beta weights (β) and the noise covariance matrix obtained from the first level statistical model for each subject, condition (spontaneous and volitional) and source–detector pair were then used in a group-level mixed effects model. This is described in Wilkinson's notation as: $\beta \sim -1 + \text{condition} + (1|\text{subject}) + \epsilon$, and allows us to use the full covariance from the first level to perform a weighted least-squares fit and account for the fact that the noise measured in our channels may vary across the array and across subjects. Both the canonical and finite impulse response (FIR) hemodynamic responses were calculated and demonstrated a similar pattern of functional hemodynamic response, but a clear global signal was also evident. A baseline principal component analysis (bPCA) filter was applied to reduce spatial covariance (Franceschini et al., 2006). Results were then corrected using the Benjamini-Hochberg procedure (Benjamini & Hochberg, 1995). The hemodynamic response functions and significant t-statistics for the separate chromophores for each condition are shown in Supplementary Fig. 2 and Supplementary Tables 4 and 5.

For a channel to demonstrate a significant activation in response to a given stimulus, three conditions had to be met. First, the changes in the concentrations of HbO and HbR in response to each stimulus could not significantly differ from the canonical model (HbO had to increase and HbR decrease) as determined by the application of AR(P)-IRLS (Barker et al., 2013). Second, the Hotelling's t^2 test (Hotelling, 1992) was used to determine if a channel demonstrated a response in which HbO and HbR, when taken together, are significantly different from baseline at $p < .005$ (after correcting for multiple comparisons) (Benjamini & Hochberg, 1995). The null hypothesis for Hotelling's t^2 test is that there would be no change in signal given the joint probability of oxy- and deoxy-hemoglobin concentration. Channels that met this criteria (Supplementary Tables 2 and 3) were then projected onto the Colin-27 atlas using a Monte-Carlo photon-transport model (Fang & Boas, 2009; Holmes et al., 1998). The calculation of both Hotelling's t^2 test joint statistics (Fig. 4) and t-statistics for HbO and HbR (Fig. 5) compared to baseline provides a more complete picture of functional activation.

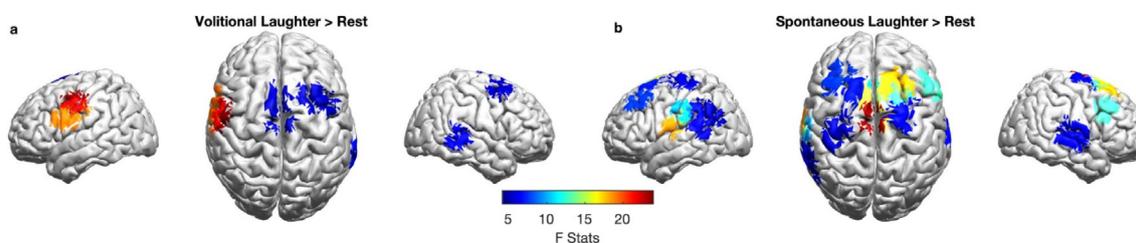


Fig. 4 – The F statistics and their level of significance produced by Hotelling's t^2 joint test. This is used to determine if the changes in HbO or HbR in combination are significantly different from baseline (rest). Significant responses were projected onto the cortex for (a) volitional laughter and (b) spontaneous laughter at a 10% threshold at $p < .005$.

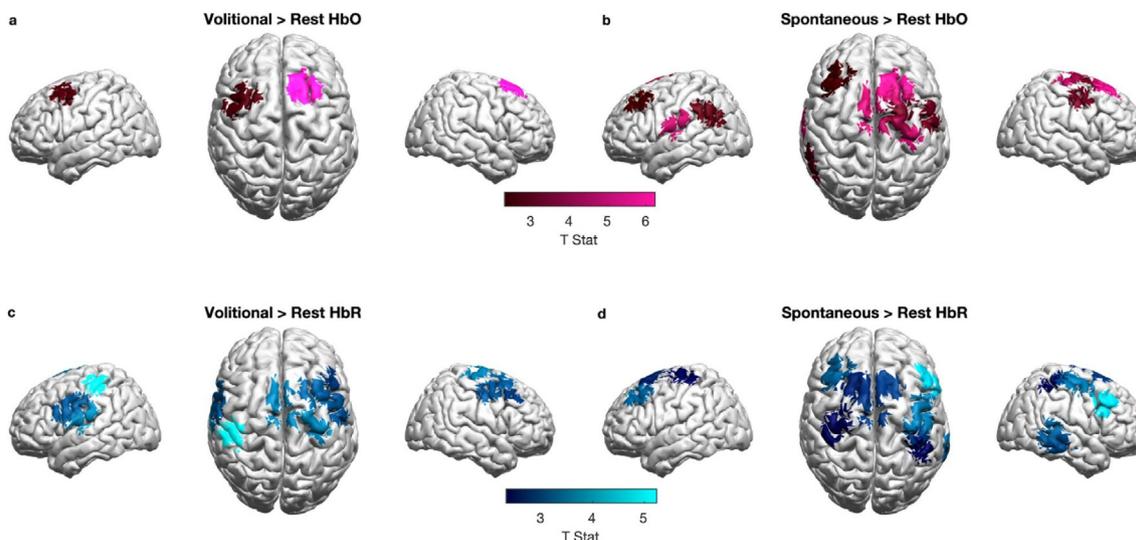


Fig. 5 – The results of the t-tests on β values produced by the GLM. Significant responses were projected onto the Colin-27 atlas demonstrating regions of significance at a 10% threshold at $p < .05$. Where responses were greater listening to volitional than that for rest are shown in the first column (a,c). Regions where the spontaneous activation was greater than that for rest are shown in the second column (b,d).

As seen in Fig. 4a both laughter types activate regions in the right temporal lobe, but only spontaneous laughter results in activation of the posterior portion of the left temporal lobe. The superior portion of the temporal lobe is a key node in auditory processing of complex sounds, such as vocalizations (Scott, 2019). In agreement with our findings, the right superior temporal gyrus has been shown to respond to spontaneous laughter sounds in order to process the socially-relevant information (McGettigan et al., 2015; O'Nions et al., 2017; Wildgruber et al., 2013). Specifically, the superior temporal gyrus has been shown to be capable of discriminating between emotional and neutral prosodies (Zhang et al., 2018), and non-emotional and flat prosody (Kyong et al., 2014).

Additionally, both types of laughter elicit activation in the pre-SMA and SMA; however, this activity is stronger and more widely distributed for spontaneous laughter. In humans and macaques there is a rough somatotopic organisation within the pre-SMA and SMA, and the face/mouth area is on the border between the two regions (Lima et al., 2016). The left DLPFC was significant for the contrast of spontaneous laughter > rest, and has been shown to function as a key regulator of emotional attention (De Raedt et al., 2015; Sanchez-Lopez et al., 2018). Our results also support the

greater activation of the right IFG in the processing of spontaneous laughter, which is in accordance with the literature related to the explicit processing of spontaneous laughter sounds (O'Nions et al., 2017). The left IPL was significantly active for spontaneous laughter > rest. The left IPL supports socio-cognitive processes and has been implicated in the Theory of Mind networks (Aichhorn et al., 2008; Saxe & Kanwisher, 2003; Schurz et al., 2017). Previous work has demonstrated the IPL's relationship between behavioural gain and classification accuracy for the type of emotional sound (Kreifelts et al., 2007). Additionally, the left IPL is associated with the ability to differentiate between self and others, which would be critical for understanding the correct laughter response (Vogeley & Fink, 2003).

Fig. 4 shows activation within the left somatosensory cortex that is greater in response to spontaneous laughter, but when examining the chromophores separately in Fig. 5 there is evident bilateral activation for both laughter types. The recruitment of the sensorimotor cortex has been argued to support the perception of social cues, as part of higher order mechanisms for the social and emotional understanding of others (Carr et al., 2003; McGettigan et al., 2015; Warren et al., 2006). Both of the contrasts for volitional laughter > rest and

spontaneous laughter > rest reveal activation in the right primary motor area for HbR (Fig. 5 c,d), but they are not strong enough to produce significant F statistics when combined with HbO (Fig. 4). The activation of premotor and motor regions in response to hearing laughter is thought to facilitate joining in with other's laughter to promote greater feelings of social connectedness (Gervais & Wilson, 2005; Warren et al., 2006). The contrast of volitional laughter > rest resulted in activations within regions associated with the intentional production of vocalisations, including the left IFG, and ventral portion of the premotor and motor cortex (Uwe Jürgens, 2002).

Similar patterns of activation remain when contrasting the two laughter types against each other (Fig. 6). We set two constraints on this analysis for a channel to be considered significant. As was the case in the previous analysis, the direction of the HRF for each chromophore could not significantly differ from that of the canonical HRF. Second, the channel in question must have significantly different activation for that condition. The HbO contrast for volitional > spontaneous resulted in only one significant channel, which sampled from the left middle frontal gyrus (Fig. 6a). This contrast for HbR produced similar results to the volitional > rest condition (Fig. 5 a,c). There was prominent activation in the left mouth pre-motor and motor regions. Bilateral dorsal sensorimotor activation occurred in volitional > spontaneous as well as spontaneous > volitional in channels that were adjacent to each other. This suggests that to determine gyral activation a masking ROI approach would be valuable, but the spatial resolution of this fNIRS array would not be conducive to such an approach. The spontaneous > volitional contrast revealed significant activation for both chromophores in a channel associated with the pre-SMA. This channel had been activated by volitional > rest for HbO, but to a much smaller degree. Both chromophores for the contrast spontaneous > volitional were activated in the left DLPFC. Lastly, this contrast showed

activations in the left IPL, left SMA and right temporal lobe consistent with spontaneous > rest (Figs. 5b,d and 6b,d).

3.3. Cortical activation modulates behavioural ratings

Based on our hypothesis regarding variances in neuronal activation that result in characteristic behavioural ratings, we then tested if the differences between hemodynamic responses for spontaneous and volitional laughter were correlated with the distinction in ratings for authenticity and contagion. For each subject, their average contagion rating for volitional laughter was subtracted from their average contagion rating for spontaneous laughter. Their individual F-statistics for both types of laughter compared to baseline were computed in the method described in section 3.2. The F-statistic for volitional laughter was subtracted from the F-statistic calculated for spontaneous laughter, meaning that each individual was now represented by 2 terms: one representing differences in neuronal activation to the two types of laughter and the other for differences in contagion ratings for both types of laughter. For each channel, a stepwise general linear regression model was used to test if the effect of the neural activation term on the behavioural rating term across all of the subjects. The same analysis was run for authenticity ratings and F-statistics.

After correcting for multiple comparisons, we found that localised activation in the pre-SMA predicted the differences in both authenticity and contagion ratings for spontaneous laughter compared to volitional. The influence of the pre-SMA activity on authenticity ratings was stronger than contagion, and this difference was significant at $p < .0005$ (Supplementary Tables 8 and 9). The pre-SMA has previously been implicated in the contagious effect of laughter, including a study that showed that boys who are at risk of psychopathy had reduced pre-SMA and SMA activation in response to laughter, and a decreased urge to join in (O'Nions et al., 2017). Example data

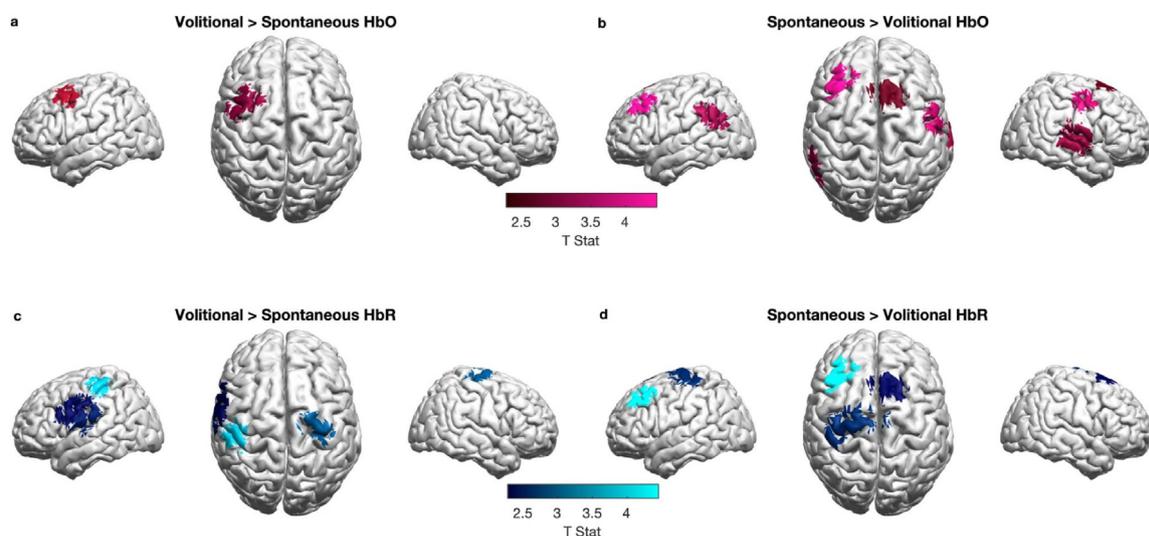


Fig. 6 – The results of the t-tests on β values produced by the GLM. Significant responses were projected onto the Colin-27 atlas demonstrating regions of significance. Where responses were greater listening to volitional than that for spontaneous are shown in the first column (a,c). Regions where the spontaneous was greater than that for volitional laughter are shown in the second (b,d).

for a significant pre-SMA channel (Fig. 8a,c) and an insignificant channel in the right inferior temporal lobe (Fig. 8b,d) are shown. The positive slope seen in the right inferior temporal lobe plots appears to be reduced by the single more negative point Fig. 7.

4. Discussion

Sharing emotions within a group leads to greater feelings of cooperation, cohesiveness, and social connectedness (Gervais & Wilson, 2005; Warren et al., 2006). Social behaviour disorders, such as autism spectrum condition (ASC) and schizophrenia, are often characterised by marked differences in how individuals process or produce laughter (Hudenko et al., 2009; Hudenko & Magenheimer, 2012; Reddy et al., 2002). Therefore, studying laughter is relevant as a potential method for the diagnosis of ASC, as there are known differences in affect

sharing and the mentalizing ability of children with ASC, especially with regards to non-verbal vocal communication (Frith & Frith, 2012). For example, it is extremely important for a child's behavioural development that they understand the difference between laughing with other children and being laughed at by those around them. Laughter also provides an outstanding opportunity to study social cognition because it is culturally universal and not dependent on language (Bryant et al., 2016; Sauter et al., 2010; Scott et al., 2014).

The theory that we automatically imitate the people around us to better understand their emotions and intentions was published more than a hundred years ago (Lipps, 1903). Nevertheless, technological advances have facilitated numerous studies which indicate the existence of an auditory-motor mirror network that aids in the processing and appropriate response to behaviourally contagious emotional stimuli. These include both primate studies (Fogassi et al., 2005; Keysers et al., 2003; Kohler et al., 2002) and

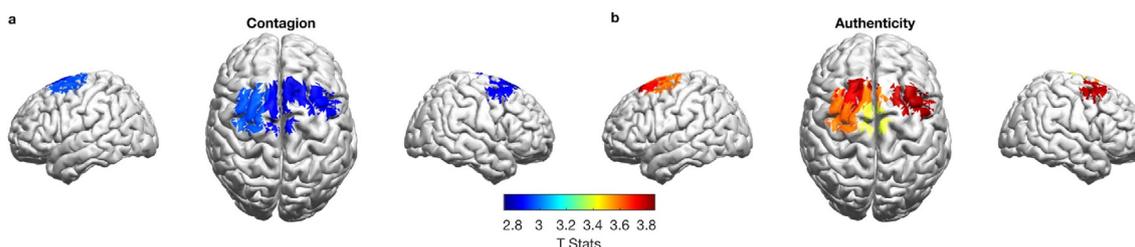


Fig. 7 – A regression analysis was used to model the correlation between type-dependent differences in hemodynamic activity (F statistics from the previous analysis) and the differences in behavioural ratings for (a) contagion and (b) authenticity. T statistics that survived multiple comparisons at $p < .05$ were projected onto the cortex at a 10% threshold.

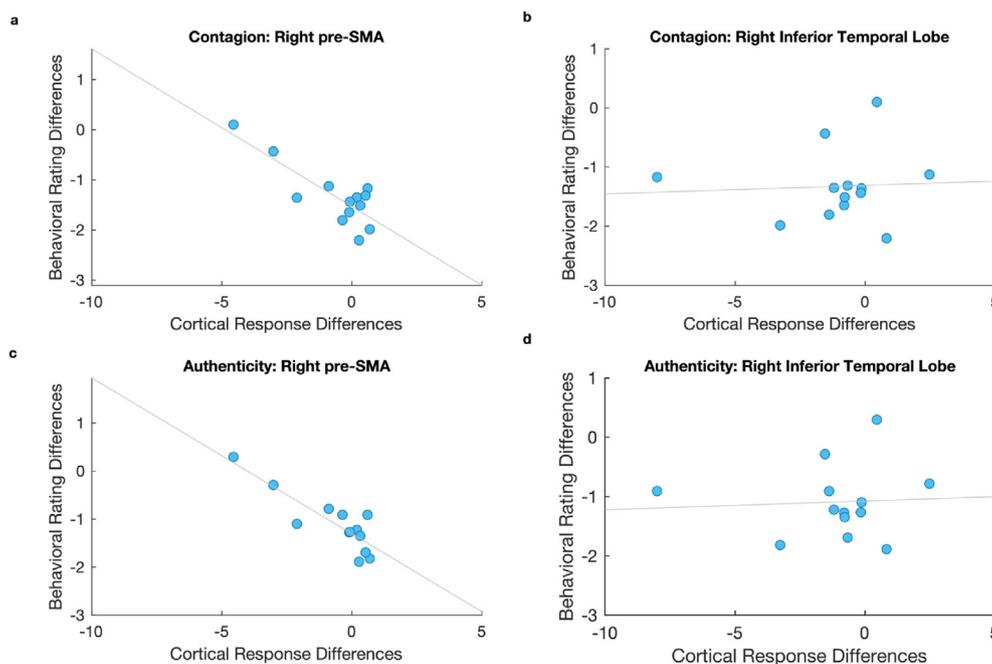


Fig. 8 – Selected channels to demonstrate the difference between pre-SMA activation and other cortical areas. A stepwise linear regression model was for each channel for authenticity and contagion measurements to determine the relationship between cortical response differences and behavioural rating differences.

human brain stimulation work (Aziz-Zadeh et al., 2004; Fadiga et al., 2002).

McGettigan and colleagues' study which used fMRI for laughter perception showed significantly positive psychophysiological interactions (PPIs) related to this network. A PPI with the left somatosensory cortex revealed responses in the right IFG, left SMA, and left parietal operculum, and right superior occipital cortex for real laughter compared to posed laughter for the correct detection of authenticity. A PPI was also calculated with the left pre-SMA indicated that the pre-SMA influenced the activity in the bilateral pre-SMA, bilateral cuneus, left caudate nucleus, bilateral primary cortex, bilateral SMA and left somatosensory cortex (McGettigan et al., 2015). The main effects of the study, which looked at how individual differences in the level of engagement of the sensorimotor cortex predicted the accuracy in judging the levels of authenticity of the laughter sounds, also support the hypothesis for orofacial mirroring network in the context of emotional contagion (McGettigan et al., 2015). These results are in agreement with a study by Warren et al., which established that the perception of emotional vocalisations engaged the auditory-motor mirror system (Warren et al., 2006). This effect was significant, even though Warren used only volitional emotional tokens which are less contagious.

Our results demonstrate that regions affiliated with the auditory-motor mirror system are recruited when processing laughter sounds. The auditory-motor mirror system may selectively map specific heard actions onto the motor programmes for executing the same auditory actions, which may be why it is activated differently for different laughter types (Gallese et al., 1996; Keysers et al., 2003; Kohler et al., 2002). We also show that spontaneous laughter is rated as more contagious and authentic than volitional laughter, and that those differences in ratings are correlated with activity within the pre-SMA. We note a strong ceiling effect for contagion ratings of the spontaneous laughter: further studies which modulate the arousal of the laughter, as well as its volitional/spontaneous nature, may well be a way of exploring this further (Lavan et al., 2018).

A previous study of smiling has shown similar effects. Leslie and colleagues showed their participants photographs of other people smiling or frowning, and participants were instructed to either imitate the facial expression or to simply view it (Leslie et al., 2004). They found that viewing the photographs activated the affective network, including the left parietal operculum, right superior temporal gyrus, pre-SMA, and premotor regions. Imitation of the expressions activated these regions, with the addition of the left ventral premotor region, the left IFG pars opercularis, and the bilateral mouth motor area. This suggests that viewing the emotional expressions results in an unconscious engagement of the network, but that conscious imitation also requires left-lateralised premotor and motor engagement in the mouth region. Our results showing the selective activation of the left IFG, ventral premotor and mouth regions of the sensorimotor cortex demonstrate the specificity of the network for different types of stimuli. The pre-SMA is connected to the ventral aspects of the PMC (Halsband et al., 1994). This activation supports the link between volitional laughter and speech, referred to as

“laughspeak” by Robert Provine (Provine, 2001; see also; Scott et al., 2014). These cortical mouth areas are necessary to articulate planned laughter, and have been shown to contain selective mirror responses to mouth actions and hearing vocal sounds (Gazzola et al., 2006; Jabbi & Keysers, 2008). As volitional laughter is more closely associated with language, our results are supported by the finding that listening to speech modulates the excitability of the tongue muscles (Fadiga et al., 2002). Stimulating the ventral portion of the premotor cortex elicits smiling and laughter, but participants report that it is not associated with any emotions (Caruana et al., 2015, 2020). This region is primarily involved in the control of volitional sounds, not emotional ones. Moreover, the left IFG is associated with the initiation of verbal responses while the right IFG, AI and pre-SMA play inhibitory roles (Xue et al., 2008).

Humans find both types of laughter contagious. As seen Fig. 2 for contagion ratings we had 266 responses and of those only .01% were rated a 1, .008% were rated a 2 and .075% were rated a 3. In analysing the effect of differences in hemodynamic activity on the differences of behavioural ratings, there were significant differences in the pre-SMA for contagion and authenticity. We conclude that the pre-SMA is involved in motor control and representation for contagion, but not in the emotional aspects of the mentalizing network. Further evidence for this view is a lack of opioid release during laughter within the pre-SMA (Caruana, 2017). Moreover, simply stimulating the pre-SMA is enough to produce laughter sounds (Fried et al., 1998). Krolak-Salmon et al., showed that when they stimulated the left pre-SMA their participant smiled, laughed, and reported feelings of happiness (Krolak-Salmon et al., 2006). They found that the same region responded to the observation of happy faces, and the authors concluded that the mirror-like activity of the region may be critical for understanding social cues, as well as responding appropriately. Taken together, these results point to the role of the pre-SMA as a facilitator of emotional contagion and a precursor of emotional empathy.

Literature on the functional connections to and from the pre-SMA indicate that the emotional aspects of laughter processing and production originate in the ACCg (Jürgens, 2002; Lima et al., 2016; Liu et al., 2002). Stimulation studies show that it elicits feelings of mirth, causes laughter, and is active during the observation of other's laughter (Caruana et al., 2015, 2018, 2020; Sperli et al., 2006). The ACC projects to the pre-SMA through the anterior cingulate bundle (Gerbella et al., 2021). Macaque studies have shown ACC receives input from the right STS/STG (Sallet et al., 2011). Our results also indicate an increased superior temporal lobe activation in response to spontaneous laughter compared to volitional (McGettigan et al., 2015; O'Nions et al., 2017).

Similarly to other contagious behaviours, laughter is a reflection of the degree of closeness of relationships as well as social structure (Bryant et al., 2016; Hurley et al., 2011). While behavioural contagion may aid mentalising, it is still dependent on the integration of other social cues. A recent study showed that mirroring behaviours are modified by group membership, and this was represented neuronally within the affective sharing network (Krauthaim et al., 2019). Interestingly, the group membership contrast affected the right pre-

SMA most strongly. The pre-SMA is involved in the preparation, initiation and inhibition of actions, and is mediated by higher-order regions such as the mPFC that provide contextual information (Jahn et al., 2016; Luppino & Rizzolatti, 2000; Nachev et al., 2008).

4.1. Limitations and future works

The value of a tool is determined on an application-specific basis. For studying social behaviour, optical neuroimaging methods have enormous potential, as they balance ecological validity with spatial and temporal resolution. Our results are consistent with similar studies performed with fMRI (McGettigan et al., 2015; O’Nions et al., 2017), demonstrating that fNIRS can be reliably used to test the neural correlates of social behaviour. However, our test was conducted with a limited field of view due to array size and lack of depth sensitivity.

Unfortunately, due to the limited cortical depth of fNIRS we were not able to test the ACCg, which is known to be related to the expression of emotional vocalisations of humans and monkeys and acts independently of the intentional vocalisation pathway (Holstege & Subramanian, 2016; Jürgens, 2009; McGettigan et al., 2015). Other areas that are implicated in laughter processing and production were not possible to test due to their location, including the mPFC, temporal poles, PAG and the nucleus accumbens (Jürgens, 2002; McGettigan et al., 2015; O’Nions et al., 2017). It has also been shown that laughter modulates the mesolimbic reward centres (Mobbs et al., 2003) and relating it to the differences in spontaneous and volitional laughter would be a potential future direction for the field.

Emerging optical neuroimaging technologies provide a wider field of view and improved sampling density, which increases spatial resolution and reduces sensitivity to physiological noise (Frijia et al., 2020). As these technologies are also more wearable, the next study will utilize these to study infant development. Lastly, in this study, we did not include the production of laughter, so it was not possible to directly test the auditory-motor mirror network’s involvement in laughter processing. Therefore we can only conclude that the processing of laughter sounds engage regions known to be associated with the network. Lastly, no part of the study procedures or analyses were pre-registered prior to the research being conducted.

5. Conclusion

We used fNIRS and questionnaire data to investigate the processing of spontaneous and volitional laughter on a neurological and behavioural level. This is the first study to show that the differences in a person’s ratings of a laughter sound in terms of authenticity and contagion is predicted by the levels of neural response induced by the different laughter types within the pre-SMA. Our results show that understanding emotions in others may involve neural structures implicated in the auditory-motor mirror network. Lastly, our findings demonstrate the importance of using appropriate

statistical methodologies and the benefits of emerging fNIRS technologies. All raw data can be found at <https://osf.io/raxh8>.

Credit author statement

Addison Billing: conceptualization, methods, software, formal analysis, resources, project admin, writing-original, writing-reviewing and editing. **Robert Cooper:** methods, software, investigation, writing- review and editing. **Sophie Scott:** conceptualization, methods, resources, writing- editing and reviewing.

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Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.cortex.2021.06.010>.

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