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Decoding brain basis of laughter and crying in natural scenes

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ABSTRACT

Laughter and crying are universal signals of prosociality and distress, respectively. Here we investigated the functional brain basis of perceiving laughter and crying using naturalistic functional magnetic resonance imaging (fMRI) approach. We measured haemodynamic brain activity evoked by laughter and crying in three experiments with 100 subjects in each. The subjects i) viewed a 20-minute medley of short video clips, and ii) 30 min of a full-length feature film, and iii) listened to 15 min of a radio play that all contained bursts of laughter and crying. Intensity of laughing and crying in the videos and radio play was annotated by independent observes, and the resulting time series were used to predict hemodynamic activity to laughter and crying episodes. Multivariate pattern analysis (MVPA) was used to test for regional selectivity in laughter and crying evoked activations. Laughter induced widespread activity in ventral visual cortex and superior and middle temporal and motor cortices. Crying activated thalamus, cingulate cortex along the anterior-posterior axis, insula and orbitofrontal cortex. Both laughter and crying could be decoded accurately (66–77% depending on the experiment) from the BOLD signal, and the voxels contributing most significantly to classification were in superior temporal cortex. These results suggest that perceiving laughter and crying engage distinct neural networks, whose activity suppresses each other to manage appropriate behavioral responses to others' bonding and distress signals.

1. Introduction

Humans have an urgent need to feel belonging to groups and use a multitude of expressions for signifying this. Laughter is a universally recognized positive social expression. It occurs frequently in human social interactions (Sauter et al., 2010; Scott et al., 2015) but is also common among nonhuman primates (Preuschoft, 1992; Ross et al., 2009) and rodents (Panksepp and Burgdorf, 2003). Macaques and chimpanzees use a quiet smile-like gesture to appease aggressive conspecifics, whereas relaxed open-mouth vocalizations are associated with both play behavior and pair formation (Preuschoft, 1992; Waller and Dunbar, 2005). Similarly, humans use quiet smiles for signaling social approval and openness to social interaction (Calvo et al., 2012; Calvo and Nummenmaa, 2015), whereas laughter is used more directly for promoting social bonding (Dunbar, 2012; Scott et al., 2015). Functional and acoustic properties of this kind of play signals in humans resemble those of numerous other animals, most notably other great apes (Winkler and Bryant, 2021).

Laughter is a powerful mechanism for bonding, as it is highly contagious (Provine, 2004) allowing the bonding response to spread throughout the interacting group to increase the effectiveness of this type of 'vocal grooming' (Dunbar, 2012). Accordingly, behavioral work suggests that a shared sense of humor is indeed a strong predictor of affiliation and altruism (Curry and Dunbar, 2013). Human molecular imaging studies in turn have shown that the bonding function of laugher is governed by the endogenous opioid system (Manninen et al., 2017; Sun et al., 2022) that modulates both pleasurable and calm sensations (Nummenmaa and Tuominen, 2018; Kantonen et al., 2020) thus signaling safety in close proximity with important others. Crying is also used for signaling the need for social contact, but unlike laughter it is evoked when social losses or social distancing is experienced. This kind of cue engages the putative separation distress circuit in the mammalian brain that consequently modulates approach behavior and social contact seeking (Panksepp, 2003). Due to the centrality attachment in mental health and well-being, it is critical to understand the functional systems processing of these distinct types of social attachment signals.

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Fig. 1. Experimental setup. The subjects viewed a medley of 96 movie clips (mean duration 12.5 s) in a fixed order (Experiment 1), 30 min of a featuee film (Experiment 2) and listened to 15 min of radio play (Experiment 3). Intensity of laughter and crying in the movie clips was annotated at 0.25 Hz temporal resolution.

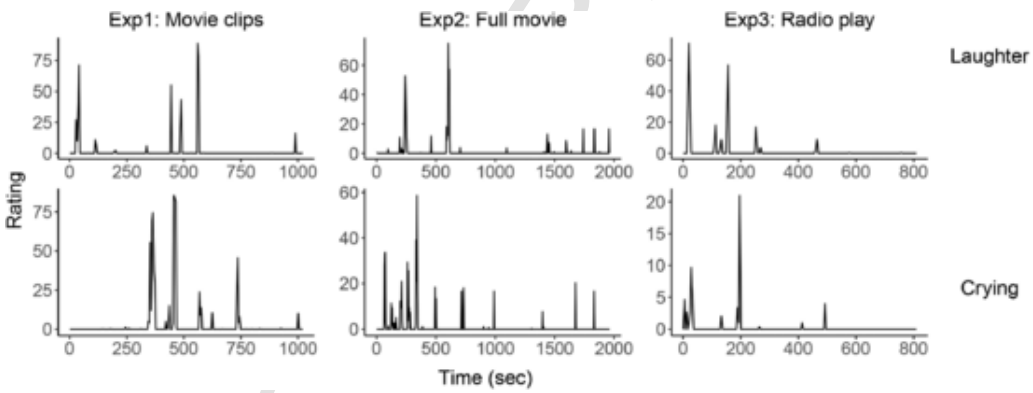

Fig. 2. Time series for the laughter and crying regressors in each experiment.

Despite significant interest in the neurobiology of human facial expression perception, there is a surprising paucity of data on the neurobiology of the social bonding circuits engaged by laughter and crying. This is saliently illustrated by the fact that the most widely used sets of static and dynamic human facial emotional expressions (Ekman and Friesen, 1976; Lundqvist et al., 1988; Tottenham et al., 2009; van der Schalk et al., 2011) explicitly exclude laughter and crying from the expression categories. Although happy and sad facial expressions could be interpreted as low-intensity variants of laughter and crying, it is likely that the full-blown, multisensory communicative information conveyed by laughter and crying is different than that contained in simple facial expressions, and possibly also processed via disctinct neural circuitry. In line with the paucity of experimental stimulus databases, the NeuroSynth database for fMRI activation meta-analysis (Yarkoni et al., 2011) does not contain a sufficient number of studies for generating meta-analysis for terms "laughter" or "crying". This is in stark contrast with studies on the canonical basic emotions (angry: 159, disgust: 103, fear: 363, happy: 225, sad: 163 studies per April 15th 2021). The extant literature however shows that laughter generation involves the motor cortex, supplementary motor area as well as the limbic the regions such as the anterior cingulate cortex, amygdala, nucleus accumbens, and hippocampus. Further modulatory systems include basal ganglia, thalamus, and cerebellum (Talami et al., 2020; Gerbella et al., 2021).

Crying, in turn is generated via the interplay between medulla and midbrain structures as well as the hypothalamus, amygdala, insula and prefrontal cortices (Newman, 2007; Bylsma et al., 2019). Functional imaging studies have established that hearing adult laughter and crying activates the amygdala, insula, and auditory cortices (Sander and Scheich, 2001; Sander et al., 2003, 2005; Fecteau et al., 2007). Pattern recognition studies have also found that vocal affect bursts including laughter and crying can be successfully decoded from the brain activity in the auditory and inferior frontal cortices (Kotz et al., 2013; Paquette et al., 2018). These, typically very focal, effects are in stark contrast with the widespread activation of limbic and paralimbic circuits typically activated during emotional episodes (Kober et al., 2008; Nummenmaa et al., 2012, 2014) and whose activity can also be used for decoding the specific emotion state of an individual (Kragel and Labar, 2015; Kragel et al., 2016; Saarimäki et al., 2016, 2018). Altogether these data suggest that acoustic social signal perception is at least partially decoupled from the engagement of the large-scale circuits generating affective responses.

1.1. The current study

Both laughter and crying occur in complex, dynamic social settings with variable and dynamically evolving time courses. However, all the previous studies on laughter and crying have measured brain responses to isolated crying and laughter segments that are not representative of the dynamic and ever-changing real world. Accordingly, it can be questioned whether these data generalize to the processing of complex and dynamic real-world affiliative behavior (Adolphs et al., 2016). Here we measured brain responses to laughter and crying and validated their

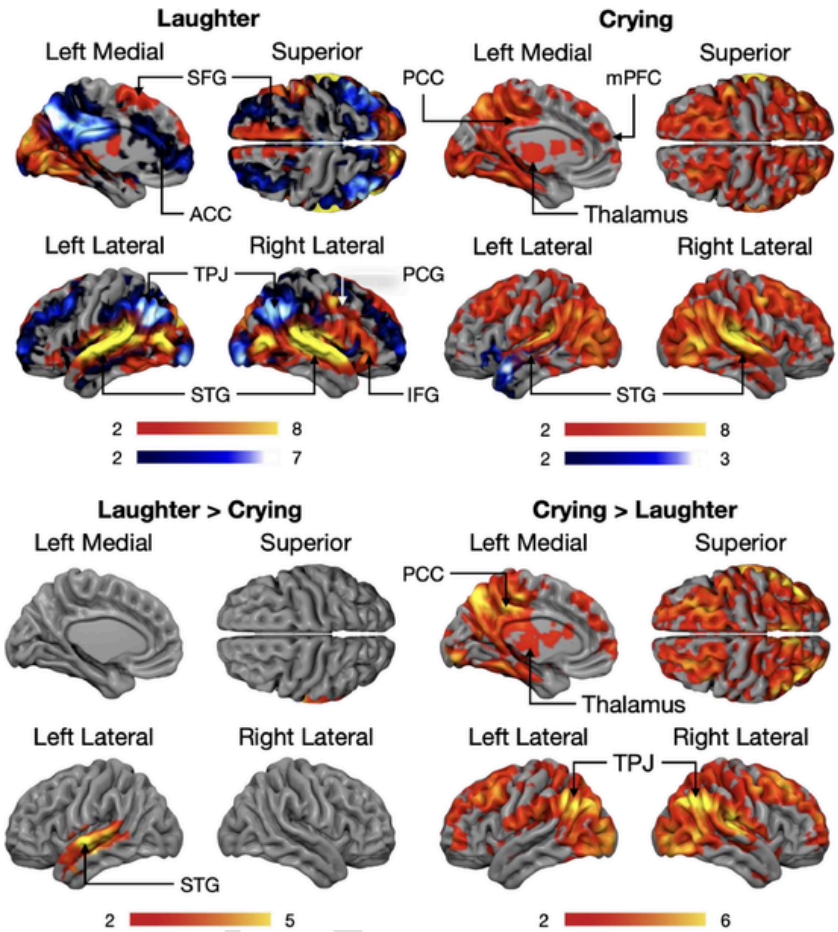

Fig. 3. Brain responses to crying and laughter across all experiments. The data are thresholded at $p < 0.05$ FWE corrected. Colourbar shows the t-statistic range (hot = positive, cool = negative). ACC = Anterior Cingulate Cortex, IFG = Inferior Frontal Gyrus, mPFC = Medial prefrontal cortex, PCC = Posterior cingulate, PCG = Precentral Gyrus, STG = Superior Temporal Gyrus, TPJ = Temporo-Parietal Junction.

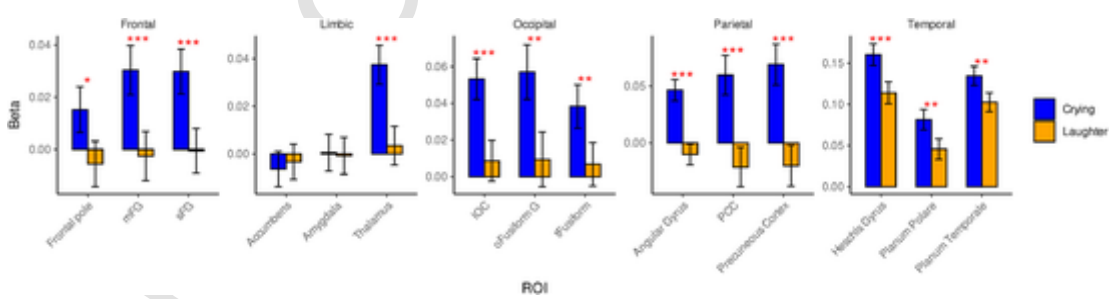

Fig. 4. Regional responses (betas) to laughter and crying across all experiments. * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$. IOC = inferior occipital gyrus, mFG = middle frontal gyrus, oFusiformG = Occipital Fusiform gyrus, PCC = posterior cingulate, sFG = superior frontal gyrus, tFusiform = Temporal Occipital Fusiform Cortex.

consistency in three large-scale (n = 100) fMRI experiments. We measured haemodynamic brain activation and presented our subjects with audiovisual episodes containing naturalistic laughter and crying in medley of short video clips with no consistent narrative (**Experiment 1**) as well as in the context of a feature film with strong plotline (**Experiment 2**). Additionally, naturalistic audio-only laughter and crying episodes were presented in the context of a radio play with a clear plotline (**Experiment 3**). We show that all experiments yielded reliable and dissociable responses to laughter and crying. Statistical pattern recognition further allowed accurate classification of laughter and crying episodes, with voxels in the auditory cortices contributing most consistently to the classification.

2. Methods

Altogether 102 volunteers (51 females, mean age 31 years, range 20–57 years) participated in the study and completed all the three experiements. The exclusion criteria included a history of neurological or psychiatric disorders, alcohol or substance abuse, current use of medication affecting the central nervous system and the standard MRI exclusion criteria. Two additional subjects were scanned but excluded from further analyses because of unusable MRI data due to gradient coil malfunction. All subjects gave an informed, written consent and were compensated for their participation. The ethics board of the Hospital District of Southwest Finland had approved the protocol and the study was conducted in accordance with the Declaration of Helsinki.

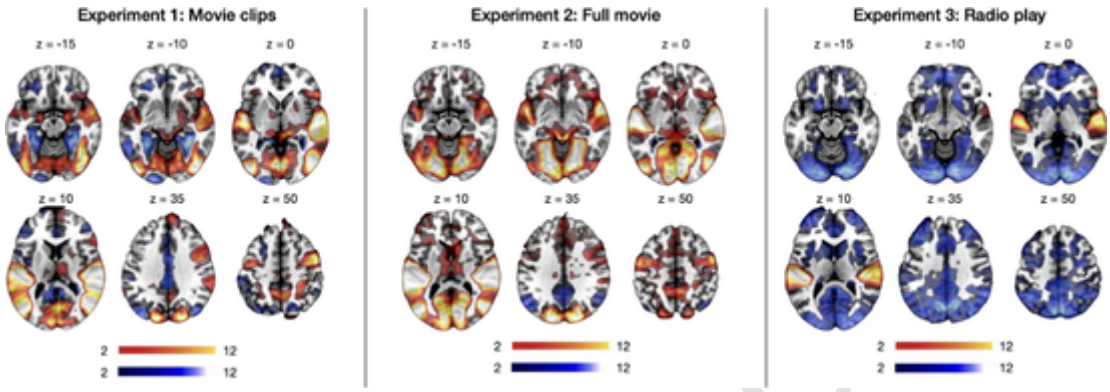

Fig. 5. Brain responses to laughter in each experiment. The data are thresholded at $p < 0.05$ FWE corrected. Colourbar shows the t-statistic range (hot = positive, cool = negative).

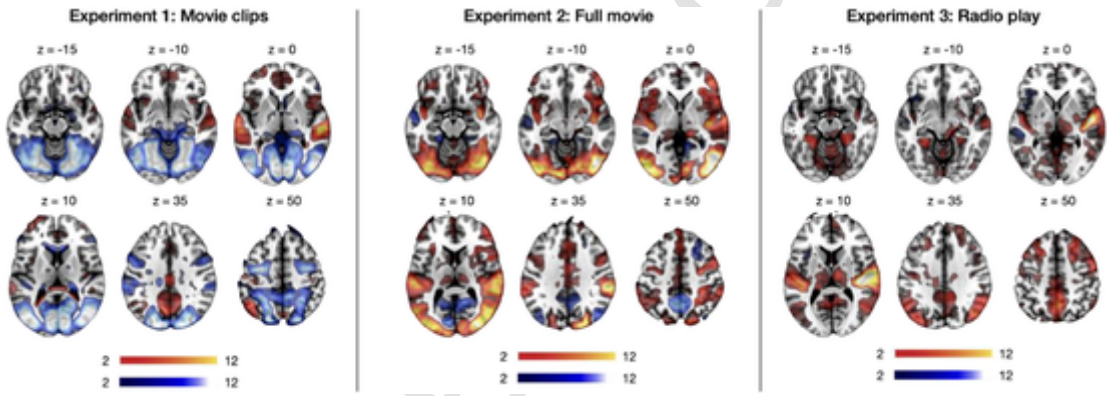

Fig. 6. Brain responses to crying in each experiment. The data are thresholded at $p < 0.05$ FWE corrected. Colourbar shows the t-statistic range (hot = positive, cool = negative).

2.1. Experimental design

Three experiments were conducted to map the brain basis of perceiving natural laughter and crying and all subjects completed all the experiments. First, to map responses to natural audiovisual laughter we used our previously validated movie viewing paradigm in which the subjects viewed a compilation of 96 movie clips extracted from mainstream English language feature films (mean duration 12.5 s; total duration 20 min) containing variable emotional and non-emotional content (for details, see Karjalainen et al., 2017, 2019; Lahnakoski et al., 2012). The movie clips were presented in fixed order without breaks in between and contain no coherent plot structure when viewed after each other. Second, subjects viewed the first 30 min of the Finnish feature film *Käsky* (*The Commandment* by Aku Louhimies / Helsinki Filmi, 2008). This allowed testing for generalization of the brain responses to laughter with two independent audiovisual stimulus sets of which one contained a clear narrative structure. Third, to measure responses to naturalistic acoustic laughter only, the subject listened to the first 10 min of a radio play *Puhdistus* (*Purge*, Sofi Oksanen / Radioteatteri, 2011). Although lacking in strict experimental control, this kind of naturalistic and high-dimensional stimulation model is more representative of the social world we encounter every day than well-controlled but artificial stimuli traditionally used in neuroimaging studies (Adolphs et al., 2016). To account for potential low -level sensory confounds between laughter and crying, we extracted the basic low-level acoustic and visual features of the stimuli and contrasted the mean acoustic / visual feature levels between the laughter / crying segments in each experiment. This analysis (**Table S1**) revealed that none of the visual features different between the conditions, and for acoustic features the differences were limited to RMS crossing for the short movies and zero crossing and entropy for the long movie. Importantly, for the audiobook, none of the differences were statistically significant. This analysis suggests that although laughter and crying have different acoustic and visual characteristics, low-levels sensory features are unlikely to confound with the results.

The film clips were presented via NordicNeuroLab VisualSystem binocular display, sound was delivered binaurally via MRI-compatible headphones (Sensimetrics S14) at a comfortable level adjusted individually for each participant. During the radio play a fixation cross was shown on the screen. Subjects were instructed to attend the stimuli similarly as they were viewing a movie or listening to a podcast, other than that there was no specific task. For all the stimuli used in the three experiments, dynamic ratings with a 4 s temporal resolution were obtained for the intensity of perceived laughter and crying from a separate sample of subjects (n = 6) who did not participate in the fMRI study. The average ratings were subsequently used as regressors in GLM analysis.

2.2. MRI data acquisition

The MRI data were acquired using a Phillips Ingenuity TF PET/MR 3T whole-body scanner. High-resolution (1 mm^3) structural images were obtained with a T1-weighted sequence (TR 9.8 ms, TE 4.6 ms, flip angle 7°, 250 mm FOV, 256 × 256 reconstruction matrix). A total of 407 functional volumes were acquired with a T2*-weighted echo-planar imaging sequence (TR 2600 ms, TE 30 ms, 75° flip angle, 240 mm FOV, 80 × 80 reconstruction matrix, 62.5 kHz bandwidth, 3.0 mm slice thickness, 45 interleaved slices acquired in ascending order without gaps). Significant gross brain pathology was excluded with T2-weighted images.

Fig. 7. Confusion matrices for decoding laughter and crying in the Experiments 1–3.

2.3. Structural and functional MRI data preprocessing

MRI data were preprocessed using fMRIPprep 1.3.0.2 (Esteban, Markiewicz, et al. 2018). The following preprocessing was performed on the anatomical T1-weighted (T1w) reference image: correction for intensity non-uniformity, skull-stripping, brain surface reconstruction, spatial normalization to the ICBM 152 Nonlinear Asymmetrical template version 2009c (Fonov et al., 2009) using nonlinear registration with antsRegistration (ANTs 2.2.0) and brain tissue segmentation. The following preprocessing was performed on the functional data: co-registration to the T1w reference, slice-time correction, spatial smoothing with a 6 mm Gaussian kernel, automatic removal of motion artifacts using ICA-AROMA (Pruim et al., 2015) and resampling the MNI152N-Lin2009cAsym standard space. Low-frequency drifts were removed with a 240-s- Savitzky–Golay filter (Cukur et al., 2013).

2.4. GLM data analysis

The fMRI data analyzed in SPM12 (Wellcome Trust Center for Imaging, London, UK, (http://www.fil.ion.ucl.ac.uk/spm). To reveal regions activated by laughter and crying, a separate general linear model (GLM) was fitted to the data where the BOLD signal was modelled with the laughter / crying intensity regressors as parametric modulators. Data were analyzed in two ways: First, by modeling all three experiments together (as all subjects completed all the experiment) and second, by modeling each experiment individually to address the generalizability of the effects across the experiments. Contrast images for the main effects of laughter and crying were generated for each participant and subjected to a second-level (random effects) analysis for population-level inference. The statistical threshold was set a $p < 0.05$, FWE corrected.

To visualize and further analyze the laughter and crying dependent responses, regional effects (betas) for laughter and crying were extracted in bilateral a priori anatomical regions of interest (ROIs) in occipital (inferior occipital and fusiform gyrus), parietal (angular and posterior cingulate gyrus and precuneus), temporal (Heschl's gyrus, planum temporale, and planum polare), frontal (frontal pole, middle and superior frontal gyrus), and limbic (nucleus accumbens, amygdala, and thalamus) regions. The ROIs were defined basis on the Harvard-Oxford atlas. The betas were then subjected to repeated measures t tests to reveal significantly different regional responses to laughter versus crying.

2.5. Statistical pattern recognition

A between-subject classification of natural laughter and crying was performed in datasets from three experiments including movie clips, feature film, and radio play, separately. For the classification, one label (either laughter or crying) was assigned to each time point of the signal based on the observation and evaluation of 6 raters (see experimental design section for more details). Each dataset was divided into 10 chunks and all time-points with the same class in a chunk were considered as a single event of that class. We checked the distribution of the chunks and confirmed that timepoints with the same label were not interspersed into different chunks; otherwise temporal autocorrelation of adjacent timepoints could result in an artificially increased classification accuracy. The average chunk length was 120 s for the movie clips. 198 s for the full movie and 83 s for the radio play; overall the data contained 20 events for each subject. Chunk-wise GLM with regressors for each class (laughter and crying) was fit to the data resulting in 20 beta weights (2 classes × 10 events per class) as input for the MVPA. The beta weights were then normalized ($\mu = 0$, $\sigma = 1$) before the application of MVPA.

An SVM classifier with radial basis function (RBF) kernel was trained to identify the laughter and crying using leave-one-subject-out cross-validation, where the model was trained on the data from all except one subject and tested on the hold-out subject data. We repeated this procedure 100 times so that each subject was once considered as the hold-out subject. This analysis was performed on each experiment's dataset (movie clips, Finnish feature film, and radio play) using whole-brain images which were previously skull-striped. We performed an ANOVA feature selection to the training set within each cross-validation where 5000 voxels with the highest F-score were selected. We calculated the accuracy of the classifier by computing the proportion of correctly classified events relative to the total number of events. The MVPA analyses were performed in Python using the PyMVPA toolbox (Hanke et al. 2009).

3. Results

The 3D result maps are available on NeuroVautl at (https://identifiers.org/neurovault.image:790873). Fig. 2 shows the time series of the laughter and crying bursts in each experiment. We first ran a joint analysis across the experiments to test which brain regions are activated by laughter and crying irrespective of the stimulation type (Fig. 3). This revealed that both laughter and crying activated auditory cortices and inferior and ventral temporal cortical areas, yet the auditory responses were more clearly bilateral for laughter. Furthermore, laughter was associated with significant activation in the motor and lateral frontal cortex, and deactivations in the anterior, middle, and posterior cingulate cortices, as well as temporo-parietal junction (TPJ). Conversely, crying was associated with increased activation in the posterior cingulate and precuneus, in addition to the medial frontal and thalamic activations. Direct comparison between laughter versus crying revealed that laughter only elicited stronger activations in the left superior temporal cortex, while crying-related responses were stronger in the inferior and ventral occipital regions, throughout the parietal, temporal, and frontal cortices as well as in the thalamus (Fig. 3-4).

We next tested for the main effect of laughter and crying separately for each experiment. For laughter, this analysis (Figs. 5-6) indicated

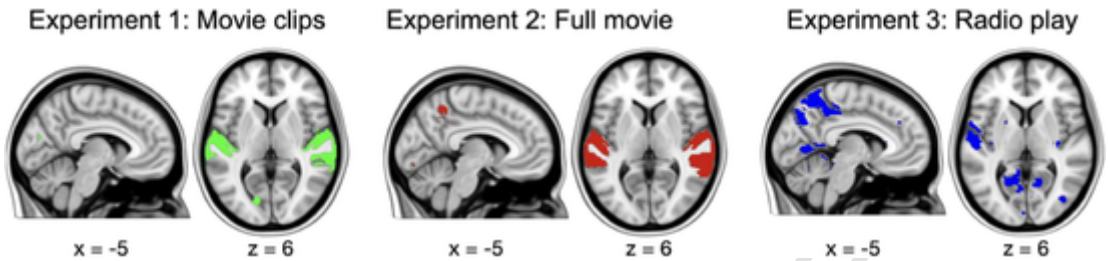

Fig. 8. Voxels contributing most significantly to the accurate classification of laughter and crying across the three experiments.

consistent activation of the auditory cortices to laughter in all the experiment. In the audiovisual experiments significant activations were also found in the brainstem, thalamus, V1, ventral temporal and lateral superior temporal cortices, somaotosensory, motor, and lateral frontal cortices. Amygdala activations were most prominent in the experiment with movie clips, whereas striatal activations were strongest in the experiment with the full movie. In the audio only experiment the responses were restricted to the auditory and right lateral frontal cortex. Crying also activated the auditory cortices consistently across experiments. Additional consistent activations were found in the posterior cingulate cortex, somatosensory cortex, and parts of the frontal and middle cingulate cortices. In the experiment with movie segments, crying resulted in large-scale deactivations in the primary visual cortex as well as throughout the temporal visual areas.

3.1. Statistical pattern recognition

Because both laughter and crying activated overlapping areas (most notably in the auditory cortex) we next assessed whether laughter and crying nevertheless elicited statistically discernible activation patterns in these and other areas. We ran the pattern recognition for the whole-brain gray matter mask, which yielded classification accuracies that significantly exceeded the permutation-based chance level. Classification accuracies generally exceeded 0.66 for both laughter and crying in all experiments (Fig. 5), being the most accurate in the experiments with audiovisual stimuli and least accurate in the audio-only experiment. The voxels contributing most significantly to accurate classification were in the auditory cortices in all the experiments, with comparable foci in the superior temporal cortices across all experiments.

4. Discussion

Our main finding was that perceiving laughter and crying from natural scenes engages distinct cortical and subcortical networks. These responses were moderately consistent across the three experiments, although in the acoustic-only experiment they were focused more narrowly on the auditory cortices. The frontoparietal and cingulate regions showed opposite activation patterns with laughter and crying, with decreased activity during laughter episodes and increased activity during crying episodes. While auditory cortices were consistently activated across experiments for laughter and crying sounds, statistical pattern recognition revealed distinct activation patterns for both vocalization types primarily in the auditory cortex. These results show that separable neural circuits are engaged in processing distinct types of social attachment cues, and that pattern recognition during dynamic scene perception allows reliable separation of laughter and crying evoked activation patterns.

4.1. Brain responses to naturalistic laughter and crying

Our data revealed that naturalistic laughter and crying evoked widespread cortical and subcortical activation patterns that extend well beyond the auditory cortices. For laughter, most prominent activations were observed in M1, lateral frontal cortex and thalamus. These effects were paralleled by significant deactivations in the anterior, middle, and posterior cingulate cortices as well as temporo-parietal junction (TPJ). The latter set of regions however showed the opposite pattern during crying sounds: These regions were significantly *more* active during the perception of the crying sounds. In addition to these regions, crying robustly activated the posterior cingulate / areas, in addition to the medial frontal and thalamic activations. This contrasts with prior unimodal studies that have found that laughter and crying evoked activations focussed primarily on the auditory cortex, amygdala, and insula (Sander et al., 2003; Wild et al., 2003; Sander and Scheich, 2005; Fecteau et al., 2007).

Grooming-based social bonding imposes constraints on the maximum possible social network size (Dunbar, 1991). Consequently, ecological pressures demanding larger group sizes have led to the evolution of more effective mechanisms for facilitating social bonding (Dunbar, 2022). Laughter is a pleasant prosocial signal that is highly contagious (Scott et al., 2015) and prior studies have indicated that laughter also induces activation of the motor and premotor areas (Lavan et al., 2017). Such "mirroring" of laughter may serve social bonding, as it presumably allows effective spreading of laughter across large crowds (Dunbar, 2012; Manninen et al., 2017), and both behavioral experiments and positron emission tomographic studies indicate that the calming effects of the laughter-evoked endogenous opioid release act as the safety signal promoting subsequent seeking of similar social contacts (Manninen et al., 2017).

We also observed significant motor cortex activation for the crying sounds. There is evidence for contagious crying and affect sharing already in infants (Simner, 1971; Geangu et al., 2010) and meta-analysis of functional imaging studies have found that perceiving infant crying activates the dorsal anterior insula, the pre-supplementary motor area and dorsomedial prefrontal cortex and the inferior frontal gyrus, as well as thalamus and cingulate cortices (Witteman et al., 2019). This kind of somatomotor "mirroring" of sadness may promote social behavior by synchronizing the thoughts and feelings across individuals, and fMRI studies using intersubject correlation analyses have indeed found that brain activation in the middle/anterior cingulate cortices becomes increasingly synchronized across individuals during negative emotional states (Nummenmaa et al., 2012, 2014). The anterior cingulate cortex is a part of the putative separation distress circuit in humans, responding to the perceived physical or affective proximity of conspecifics (Panksepp, 2003). The cingulate cortex acts as a key node of the human saliency network (Bressler and Menon, 2010), it is possible that the crying-evoked cingulate activity reflects the orienting response towards the abrupt yet socially highly relevant distress call. However, the insular cortex is also centrally involved in interoceptive processing and particularly so during emotions (Craig, 2002; Critchley and Garfinkel, 2017); the present fMRI experiments cannot however reveal which of these mutually non-exclusive roles of the insula better explains the data.

Stimulus-evoked deactivations were also observed for both stimuli and particularly for laughter. It is possible that they reflect the reflexive motor "mirroring" of laughter for bonding purposes, thus leading to dis-

engagement of the midline mentalizing networks. Similar midline deactivations were not observed consistently for crying, thus processing of others' distress might be less automatic and more contingent on slower social and evaluative processing. However, deactivations are difficult to interpret in BOLD-fMRI where the signal of interest is inherently relative, thus further studies should elaborate this issue with truly quantitative measures such as MEG or PET.

Our data indicate that laughter perception relies on somatomotor mirroring mechanisms promoting automatic laughter contagion for bonding purposes, whereas perception of crying involves more elaborate higher-order mentalizing processes. Speculatively, these differences may indicate that social laugher might have older evolutionary origins than affective crying. Indeed, comparative data suggest that evolutionary origins of human laughter can be tracked back to 10 million years ago sharing significant similarities with other hominidae (Davila Ross et al., 2009), whereas crying involving affective lacrimation is a unique human social signal which has evolved more recently (Gračanin et al., 2018).

4.2. Discrete neural signatures for laughter and crying

Across the three experiments we were consistently able to classify the presence of laughter and crying with above chance level accuracy. Unlike prior studies on vocal affect categorization (Kotz et al., 2013; Paquette et al., 2018), we classified brain signals evoked by unstructured and uncontrolled, dynamic naturalistic stimuli. Despite the complex unstructured stimulus, we nevertheless achieved high classification accuracies particularly in the audiovisual experiments. This shows how pattern recognition can be used for disentangling the specific social perceptual processes that are embedded in high-dimensional and dynamic sensory input. Voxels contributing most significantly to classification of the laughter and crying sounds were localized in the superior temporal cortices. This is in line with previous studies on decoding of auditory affective signals such as vocalizations and music, in which classification can typically be achieved in the auditory cortices (Kotz et al., 2013; Paquette et al., 2018; Putkinen et al., 2021).

Yet, these findings do not accord with patter recognition studies of emotions evoked by e.g. film clips or mental imagery, which consistently suggest discernable and emotions-specific activation patterns in the limbic and paralimbic emotion circuits (Kragel and Labar, 2015; Kragel et al., 2016; Saarimäki et al., 2016, 2018). Despite high statistical power with 100 subjects and long naturalistic experiment, we found no evidence for discernible activation patterns for laughter and crying in the limbic or subcortical regions in general. These findings can likely be reconciled by the fact that vocal expressions of laughter and crying are communicative signals rather than direct readouts of an individual's emotional state, and the corresponding acoustic-communicative differences are picked up by the multivariate classifier. Thus, it is not unexpected that their processing does not necessarily lead to emotion-specific activation in the subcortical circuits that govern affective processing similarly as for the perception of actual emotion-eliciting episodes (Nummenmaa and Saarimäki, 2017).

Although the joint analysis across the experiment indicated consistent activations for laughter and crying, some discrepancies were also observed. Most notably, effects for laughter were predominantly negative outside the temporal cortex in Experiment 3 (radio play), whereas similar effect for crying was observed in Experiment 1 (movie segments) for crying. Although we can only speculate about the reasons leading to the differential effects, these likely involve the stimulus modality (Experiments 1–2: audiovisual, Experiment 3: auditory), temporal scale aspects of the stimulus model (Experiment 1: short movie segments, Experiments 2–3: long scenes) as well as the actual stimulus contents and the frequency, type, and context of the laughter and crying episodes. Nevertheless, it must be stressed that the experiment-wise pattern classification yielded consistent results and similar regions also contributed to classification accuracy across experiments, further indicating the consistency of the laughter and crying related responses across modalities and conditions.

4.3. Limitations

Laughter is a complex social signal. Although it is used for signaling social affiliation, it can also be used to signal rejection, and laughter-evoked activations differ depending on the perceived positive versus negative intent (Ethofer et al., 2020). Also, behavioural and neuroimaging studies have revealed that humans are sensitive in spotting genuine versus volitional laughter, which also elicit distinct neural activation patterns (Scott et al., 2015; Lavan et al., 2017). Tractographic studies suggest that emotional and conversational or social laughter are subserved by partially separable neural networks (Gerbella et al., 2021). We did not specifically annotate for the type of laughter in the video clips and the radio play thus it remains unresolved how specific versus generalizable these effects are across different laughter types. Also, we deliberately used unconstrained naturalistic stimuli and did not define the stimulation a priori, but instead used subject-based annotations for deriving it. To overcome the generalizability issue pooled the data from three experiments (total duration >60 min) with 100 subjects in each, and robust GLM activations as well as significantly above-chance level classification accuracy was observed in all experiments.

Separate analysis of the three experiments revealed that the laughter and crying evoked activations were not completely consistent across different experiments (Figs. 3-6), highlighting the intrinsic variability in the naturalistic stimulus episodes occurring in the three experiments. Despite variation across experiments, the pooled GLM effects for laughter and crying (Fig. 3) can be considered as the regions that are most consistently activated while perceiving laughter and crying across variable naturalistic contexts. Finally, vocal emotional expressions may lead to facial mimicry (Hietanen et al., 1998; Volynets et al., 2020) potentially influencing motor and premotor conditions. The utilized PET-MRI scanner did not allow recording of facial movements, so this remains a potential confound. In a separate control analysis, we however correlated the head motion regressor time series against the stimulus models for laughter / crying and observed no significant associations, indicating that at least gross subject motion does not confound with the results.

Conclusions

Laughter and crying engage both shared and distinct cortical and subcortical circuits. Although they both trigger robust activation in the auditory cortex, these sensory cortical responses allow reliable encoding of the whether laugher or crying was present in the current audiovisual segment. Activity within the cortical midline network altered between laughter and crying episodes. These results suggest that perceiving laughter and crying engage distinct neural networks, whose activity suppresses each other to manage appropriate behavioral responses to others' bonding and distress signals. We propose that laughter might be a simple trigger for chorusing bonding behavior thus requiring very little mentalizing effort, whereas understanding why someone is crying is more dependent on mentalizing and higher-order social cognition.

Data and code availability statement

- Per Finnish legislation, medical images are considered as sensitive personal data and cannot be shared even after anonymization.
- Result maps have been uploaded to NeuroVault https://identifiers.org/neurovault.image:790873
- Code and stimulus materials are available from the corresponding author upon request.

Uncited link

Fig. 1, Fig. 7, Fig. 8

CRediT authorship contribution statement

Lauri Nummenmaa : Conceptualization, Methodology, Software, Writing – original draft, Writing – review & editing, Visualization, Supervision, Project administration, Funding acquisition. **Tuulia Malèn :** Conceptualization, Software, Validation, Formal analysis, Writing – original draft, Writing – review & editing, Visualization. **Sanaz Nazari-Farsani :** Conceptualization, Software, Validation, Formal analysis, Writing – original draft, Writing – review & editing. **Kerttu Seppälä :** Conceptualization, Investigation, Data curation, Writing – original draft, Writing – review & editing. **Lihua Sun :** Conceptualization, Investigation, Data curation, Writing – original draft, Writing – review & editing. **Severi Santavirta :** Conceptualization, Validation, Formal analysis, Investigation, Data curation, Writing – original draft, Writing – review & editing. **Henry K. Karlsson :** Conceptualization, Investigation, Writing – original draft, Writing – review & editing. **Matthew Hudson :** Conceptualization, Investigation, Data curation, Writing – original draft, Writing – review & editing. **Jussi Hirvonen :** Conceptualization, Investigation, Writing – original draft, Writing – review & editing. **Mikko Sams :** Conceptualization, Methodology, Writing – original draft, Writing – review & editing. **Sophie Scott :** Conceptualization, Methodology, Writing – original draft, Writing – review & editing. **Vesa Putkinen :** Conceptualization, Software, Validation, Formal analysis, Investigation, Data curation, Writing – original draft, Writing – review & editing, Visualization.

Declaration of Competing Interest

The authors declare no conflict of interest

Data availability

Per Finnis legislation medical imaging data cannot be shared even after anonymisation. Other data are available upon request.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.neuroimage.2023.120082.

References

Adolphs, R., Nummenmaa, L., Todorov, A., Haxby, J.V., 2016. Data-driven approaches in the investigation of social perception. Phil. Trans. B 371.
Bressler, S.L., Menon, V., 2010. Large-scale brain networks in cognition: emerging methods and principles. Trends Cogn. Sci. 14, 277–290.
Bylsma, L.M., Gračanin, A., Vingerhoets, A.J.J.M., 2019. The neurobiology of human crying. Clin. Auton. Res. 29, 63–73.
Calvo, M.G., Nummenmaa, L., 2015. Perceptual and affective mechanisms in facial expression recognition: an integrative review. Cogn. Emot. 1–26.
Calvo, M.G., Fernandez-Martin, A., Nummenmaa, L., 2012. Perceptual, categorical, and affective processing of ambiguous smiling facial expressions. CognitionCognition 125, 373–393.
Craig, A.D., 2002. How do you feel? Interoception: the sense of the physiological condition of the body. Nat. Rev. Neurosci. 3, 655.
Critchley, H.D., Garfinkel, S.N., 2017. Interoception and emotion. Curr. Opin. Psychol. 17, 7–14.
Cukur, T., Nishimoto, S., Huth, A.G., Gallant, J.L., 2013. Attention during natural vision warps semantic representation across the human brain. Nat. Neurosci. 16, 763. . -+.
Curry, O.S., Dunbar, R.I.M., 2013. Sharing a joke: the effects of a similar sense of humor on affiliation and altruism. Evol. Hum. Behav. 34, 125–129.
Davila Ross, M., J Owren, M., Zimmermann, E., 2009. Reconstructing the evolution of laughter in great apes and humans. Curr. Biol. 19, 1106–1111.
Dunbar, R.I.M., 1991. Functional significance of social grooming in primates. Folia. Primatol. (Basel) 57, 121–131.
Dunbar, R.I.M., 2012. Bridging the bonding gap: the transition from primates to humans. Phil. Trans. B 367, 1837–1846.
Dunbar, R.I.M., 2022. Laughter and its role in the evolution of human social bonding. Phil. Trans. B 377, 20210176.
Ekman, P., Friesen, W.V., 1976. Pictures of Facial Affect. Consulting Psychologists Press, Palo Alto, CA.
Ethofer, T., Stegmaier, S., Koch, K., Reinl, M., Kreifelts, B., Schwarz, L., Erb, M., Scheffler, K., Wildgruber, D., 2020. Are you laughing at me? Neural correlates of social intent attribution to auditory and visual laughter. Hum. Brain Mapp. 41, 353–361.
Fecteau, S., Belin, P., Joanette, Y., Armony, J.L., 2007. Amygdala responses to nonlinguistic emotional vocalizations. Neuroimage 36, 480–487.
Fonov, V.S., Evans, A.C., McKinstry, R.C., Almli, C.R., Collins, D.L., 2009. Unbiased nonlinear average age-appropriate brain templates from birth to adulthood. Neuroimage 47, S102.
Geangu, E., Benga, O., Stahl, D., Striano, T., 2010. Contagious crying beyond the first days of life. Infant Behav. Dev. 33, 279–288.
Gerbella, M., Pinardi, C., Di Cesare, G., Rizzolatti, G., Caruana, F., 2021. Two neural networks for laughter: a tractography study. Cereb. Cortex 31, 899–916.
Gračanin, A., Bylsma, L.M., Vingerhoets, A., 2018. Why only humans shed emotional tears: evolutionary and cultural perspectives. Hum Nat 29, 104–133.
Hietanen, J.K., Surakka, V., Linnankoski, I., 1998. Facial electromyographic responses to vocal affect expressions. Psychophysiology 35, 530–536.
Kantonen, T., Karjalainen, T., Isojärvi, J., Nuutila, P., Tuisku, J., Rinne, J., Hietala, J., Kaasinen, V., Kalliokoski, K., Scheinin, H., Hirvonen, J., Vehtari, A., Nummenmaa, L., 2020. Interindividual variability and lateralization of μ-opioid receptors in the human brain. Neuroimage.
Kober, H., Barrett, L.F., Joseph, J., Bliss-Moreau, E., Lindquist, K., Wager, T.D., 2008. Functional grouping and cortical-subcortical interactions in emotion: a meta-analysis of neuroimaging studies. Neuroimage 42, 998–1031.
Kotz, S.A., Kalberlah, C., Bahlmann, J., Friederici, A.D., Haynes, J.-.D., 2013. Predicting vocal emotion expressions from the human brain. Hum. Brain Mapp. 34, 1971–1981.
Kragel, P.A., Labar, K.S., 2015. Multivariate neural biomarkers of emotional states are categorically distinct. Soc. Cogn. Affect. Neurosci. 10, 1437–1448.
Kragel, P.A., Knodt, A.R., Hariri, A.R., LaBar, K.S., 2016. Decoding Spontaneous Emotional States in the Human Brain. PLoS Biol. 14, e2000106.
Lavan, N., Rankin, G., Lorking, N., Scott, S., McGettigan, C., 2017. Neural correlates of the affective properties of spontaneous and volitional laughter types. Neuropsychologia 95, 30–39.
Lundqvist, D., Flykt, A., Öhman, A., 1988. The Karolinska directed emotional faces – KDEF. CD-ROM from Department of Clinical Neuroscience. Sweden: Stockholm: Psychology section. Karolinska Institutet.
Manninen, S., Tuominen, L., Dunbar, R.I.M., Karjalainen, T., Hirvonen, J., Arponen, E., Jääskeläinen, I.P., Hari, R., Sams, M., Nummenmaa, L., 2017. Social laughter triggers endogenous opioid release in humans. J. Neurosci. 37, 6125–6131.
Newman, J.D., 2007. Neural circuits underlying crying and cry responding in mammals. Behav. Brain Res. 182, 155–165.
Nummenmaa, L., Saarimäki, H., 2017. Emotions as discrete patterns of systemic activity. Neurosci. Lett.
Nummenmaa, L., Tuominen, L.J., 2018. Opioid system and human emotions. Br. J. Pharmacol. 175, 2737–2749.
Nummenmaa, L., Glerean, E., Viinikainen, M., Jaaskelainen, I.P., Hari, R., Sams, M., 2012. Emotions promote social interaction by synchronizing brain activity across individuals. Proc. Natl. Acad. Sci. U. S. A. 109, 9599–9604.
Nummenmaa, L., Saarimaki, H., Glerean, E., Gotsopoulos, A., Jaaskelainen, I.P., Hari, R., Sams, M., 2014. Emotional speech synchronizes brains across listeners and engages large-scale dynamic brain networks. Neuroimage 102, 498–509.
Panksepp, J., 2003. Feeling the pain of social loss. Science 302, 237–239.
Panksepp, J., Burgdorf, J., 2003. Laughing" rats and the evolutionary antecedents of human joy? Physiol. Behav. 79, 533–547.
Paquette, S., Takerkart, S., Saget, S., Peretz, I., Belin, P., 2018. Cross-classification of musical and vocal emotions in the auditory cortex. Ann. N. Y. Acad. Sci. 1423, 329–337.
Preuschoft, S., 1992. Laughter" and "Smile" in Barbary Macaques (Macaca sylvanus). ethol. 91, 220–236.
Provine, R.R., 2004. Laughing, tickling, and the evolution of speech and self. Curr. Dir. Psychol. Sci. 13, 215–218.
Pruim, R.H.R., Mennes, M., Buitelaar, J.K., Beckmann, C.F., 2015. Evaluation of ICA-AROMA and alternative strategies for motion artifact removal in resting state fMRI. Neuroimage 112, 278–287.
Putkinen, V., Nazari-Farsani, S., Seppälä, K., Karjalainen, T., Sun, L., Karlsson, H.K., Hudson, M., Heikkilä, T.T., Hirvonen, J., Nummenmaa, L., 2021. Decoding music-evoked emotions in the auditory and motor cortex. Cereb. Cortex 101667. . 2020.2005.2024.
Ross, M.D., Owren, M.J., Zimmermann, E., 2009. Reconstructing the evolution of laughter in great apes and humans. Curr. Biol. 19, 1106–1111.
Saarimäki, H., Ejtehadian, L.F., Glerean, E., Jaaskelainen, I.P., Vuilleumier, P., Sams, M., Nummenmaa, L., 2018. Distributed affective space represents multiple emotion

categories across the human brain. Soc. Cogn. Affect. Neurosci. 13, 471–482.
Saarimäki, H., Gotsopoulos, A., Jääskeläinen, I.P., Lampinen, J., Vuilleumier, P., Hari, R., Sams, M., Nummenmaa, L., 2016. Discrete neural signatures of basic emotions. Cereb. Cortex 6, 2563–2573.
Sander, K., Scheich, H., 2001. Auditory perception of laughing and crying activates human amygdala regardless of attentional state. Cognit. Brain Res. 12, 181–198.
Sander, K., Scheich, H., 2005. Left auditory cortex and amygdala, but right insula dominance for human laughing and crying. J. Cogn. Neurosci. 17, 1519–1531.
Sander, K., Brechmann, A., Scheich, H., 2003. Audition of laughing and crying leads to right amygdala activation in a low-noise fMRI setting. Brain Res. Protoc. 11, 81–91.
Sauter, D.A., Eisner, F., Ekman, P., Scott, S.K., 2010. Cross-cultural recognition of basic emotions through nonverbal emotional vocalizations. Proc. Natl. Acad. Sci. U. S. A. 107, 2408–2412.
Scott, S.K., Lavan, N., Chen, S., McGettigan, C., 2015. The social life of laughter. Trends Cogn. Sci. 18, 618–620.
Simner, M.L., 1971. Newborn's response to the cry of another infant. Dev. Psychol. 5, 136–150.
Sun, L., Lukkarinen, L., Karlsson, H.K., Hirvonen, J., Tiihonen, J., Lauerma, H., Scott, S., Nummenmaa, L., 2022. Mu-opioid receptor system modulates responses to vocal bonding and distress signals in humans. Phil. Trans. B.
Talami, F., Vaudano, A.E., Meletti, S., 2020. Motor and limbic system contribution to emotional laughter across the lifespan. Cereb. Cortex 30, 3381–3391.
Tottenham, N., Tanaka, J.W., Leon, A.C., McCarry, T., Nurse, M., Hare, T.A., Marcus, D.J., Westerlund, A., Casey, B.J., Nelson, C., 2009. The NimStim set of facial expressions: judgments from untrained research participants. Psychiatry Res. 168, 242–249.
van der Schalk, J., Hawk, S.T., Fischer, A.H., Doosje, B., 2011. Moving faces, looking places: validation of the amsterdam dynamic facial expression set (ADFES). Emotion 11, 907–920.
Volynets, S., Smirnov, D., Saarimäki, H., Nummenmaa, L., 2020. Statistical pattern recognition reveals shared neural signatures for displaying and recognizing specific facial expressions. Soc. Cogn. Affect. Neurosci. 15, 803–813.
Waller, B., Dunbar, R., 2005. Differential behavioural effects of silent bared teeth display and relaxed open mouth display in chimpanzees (Pan troglodytes). ethol. 111, 129–142.
Wild, B., Rodden, F.A., Grodd, W., Ruch, W., 2003. Neural correlates of laughter and humour. Brain 126, 2121–2138.
Winkler, S.L., Bryant, G.A., 2021. Play vocalisations and human laughter: a comparative review. Bioacoustics 1–28.
Witteman, J., Van Ijzendoorn, M.H., Rilling, J.K., Bos, P.A., Schiller, N.O., Bakermans-Kranenburg, M.J., 2019. Towards a neural model of infant cry perception. Neurosci. Biobehav. Rev. 99, 23–32.
Yarkoni, T., Poldrack, R.A., Nichols, T.E., Van Essen, D.C., Wager, T.D., 2011. NeuroSynth: a new platform for large-scale automated synthesis of human functional neuroimaging data. Front. Neuroinform.