

**An investigation of Laughter and Crying:  
from behavioural, physiological and neuroimaging studies.**

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## Declaration

I, Hsi-Yi Chen, confirm that the work presented in this thesis is my own. Where information has been derived from other sources, I confirm that this has been indicated in the theses.

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## Abstract

This PhD investigates the perception of laughter and crying, two non verbal expressions of emotion, and how this perception is affected by the authenticity of the expressed emotions. Three separate approaches were used to address the perception of these stimuli by healthy participants: behavioural rating tasks, physiological responses recordings, and functional magnetic resonance imaging (fMRI) techniques. A series of behavioural ratings established that naïve listeners can reliably differentiate involuntary laughter from voluntary laughter, however, their performance was poorer when discriminating between involuntary crying and voluntary crying. In a larger set of behavioural ratings collected at the Science Museum (n=1723, age range = 3-76 years old), the ratings accuracy of voluntary and involuntary emotional vocalizations were both found to improve over age, however, the developmental trajectories of the voluntary expressions were shown to have a steeper slope throughout early adulthood than involuntary expressions. This difference may reflect a developmental learning process of perceiving voluntary emotional expressions through social interactions. The results of behavioural and developmental experiments consistently show that the involuntary crying was perceived as more similar to voluntary crying than voluntary and involuntary laughter. However the physiological responses (pupil size) shows a different pattern: listeners' pupils were significantly more dilated for involuntary vocalizations than for voluntary ones, regardless of emotions. This discrepancy between physiological responses and behavioural ratings on crying suggests that social learning processes influence the perceivers' judgments of involuntary crying, other than pure perceptual processes. In the fMRI study, we found that perceiving laughter and crying requires activation of similar areas in an emotional motor task as well as in a theory-of-mind task, suggesting that a shared interactive neural network of perceiving and interpreting emotions is involved. However, the cortical areas involved in differentiating voluntary and involuntary vocalizations are partly distinct for laughter and for crying, implying different neural networks may be responsible for the authenticity differentiation of different emotions.

In summary, this thesis demonstrates the existence of emotion-specific differences in perception of non-verbal emotional vocalizations and these differences may be due to developmental factors. Moreover, multiple neural networks were shown to play important roles in perceiving and differentiating positive and negative emotions.

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## Chapter 1 Literature review

### 1.1 Emotions

Emotions are crucial to human life, but what are emotions? Although we all think we know what emotions are, it is difficult to give an universal definition (Fehr & Russell, 1984). The nature of emotions has been described in a variety of different ways. For example, social constructivists argue that emotions are merely transitory social roles in a society, in which shared rules and expectations govern a person's emotional responses (Averill, 1980). Cognitive appraisal theorists suggest that emotions are individualised by a series of appraisals of events, so the emotions are not determined by the event *per se* but by interpretations and evaluations of a particular situation (Roseman, 1991). Some propose that emotions are biologically driven functions which evolve for dealing with fundamental life tasks such as withstanding the loss of significant others or achieving a specific goal (Ekman, 1992a).

Different research methodologies are commonly associated with theoretical arguments about what emotions are and what emotions do, whether they are socially constructed or rooted in our nature, and whether emotions exist in categories or in dimensions. For example, researchers who are more biologically oriented intend to distinguish emotions based on physiological variables (e.g., Ekman, Levenson, & Friesen, 1983) and facial muscle movements (e.g., Ekman, 2003; Ekman & Oster, 1979). However, researchers who are more culturally oriented focus on how the biological responses were evaluated and grouped by linguistic contexts and individual experience (Barrett & Russell, 1998). In fact, these two influential perspectives on emotions and their ongoing

debates since 1970 have initiated an era for our understanding of emotions, and therefore these two theoretical frameworks are briefly outlined below.

### 1.1.1 The basic emotions

A wealth of studies on emotions conducted in the past few decades have been greatly influenced by the theory of basic emotions outlined by Paul Ekman. The basic emotions were first proposed as ‘primary affects’, which includes six discrete affective states: happiness, sadness, fear, disgust, surprise, and anger (Paul Ekman & Friesen, 1969; Paul Ekman, Sorenson, & Friesen, 1969). Ekman established the theoretical framework using a wealth of empirical data across cultures and found that these basic emotions can be universally recognized from the face (Ekman & Friesen, 1971; Ekman et al., 1969). Each of these basic emotions has been demonstrated to be associated with a specific set of facial muscle movements (Ekman, Freisen, & Ancoli, 1980; Ekman & Rosenberg, 2005). The core arguments in the theory argues that these six emotions are innate and universal. Ekman later elaborated the term ‘basic’ as having distinctive characteristics in these six emotions, which have evolved to solve different fundamental life tasks (Ekman, 1992a). For example, fear, anger, disgust, and sadness were found to have distinctive patterns of physiological responses (i.e. heart rate and galvanic skin response) which were proposed to have distinct evolutionary histories (Ekman et al., 1983; Levenson, 1992). For example, to survive in various environments, a quick and unique response must prepare the body to react to different emotions, and these adaptive properties of the autonomic nervous system are viewed as evidence of supporting the emotions are innate (Ekman, 1992b; Ekman et al., 1983).

### 1.1.2 The dimensional model

From the view of the dimensional model, emotions are represented in continua and each emotion is defined relative to other emotions by similarities and differences. One important contemporary dimensional model is James Russell’s circumplex configuration model (Russell, 1980). In this model, these affective states are placed in a circular order divided by two orthogonal dimensions: pleasure-displeasure and degree of arousal. These affective states have fuzzy

boundaries which are identified by personal interpretation of input information. The interpretation that individuals are aware of becomes affective experience (Russell, 1980). According to the circumplex configuration model, the primary form of emotions is called 'core affect', commonly known as a 'feeling'. The core affect is proposed to be a neurophysiological state prior to affective experience, and individuals can consciously access to it without denoting any explicit emotion categories (e.g. fear, happiness, sadness). Any single point on the space created by the two dimensions is a core affect which can be moved around on the space by internal and external causes (Russell, 2003). The dimensional account views affective experience as being socially constructed rather than natural kinds (Barrett, 2006). Based on the constructivist view, wide spread functional neural networks can be activated as a specific constellation to a psychological state. Therefore, rather than mapping specific anatomical substrates to a specific emotion, constructivists consider a domain-general framework to subservise the emotional states (Barrett & Satpute, 2013; Lindquist & Barrett, 2012).

## 1.2 Emotions in voice

Recognition of other's emotional states plays a crucial role in social interactions, as this enhances communications by exposing underlying meaning and allows interlocutors to receive information beyond linguistic content. In addition to emotions expressed via facial expressions, bodily posture, manual gesture, and vocal cues can also communicate emotions (Atkinson, Dittrich, Gemmell, & Young, 2004; K. Scherer, 2003). Like facial expressions, vocal cues were demonstrated to have systematic properties which correlate with emotional factors: the constellations of acoustic properties of each emotional sound could predict the emotional character that participants perceived (Sauter, Eisner, Calder, & Scott, 2010). The emotional vocalisations communicating the negative basic emotions further proved to be recognised cross culturally, as were expressions of laughter (Sauter, Eisner, Ekman, & Scott, 2010), and these vocal cues were not considered as only a mirror of facial expressions (Scott, Sauter, & McGettigan, 2009). Instead, each emotional vocalization may have different types of expression that connote distinct meanings; for example, joyful laughter,

schadenfreude laughter, taunting laughter, and tickling laughter were found to well convey different kinds of emotional connotation (Szameitat et al., 2009) in native German speakers (and less so for native English speakers).

Vocal cues are effective for conveying emotional information, and moreover the vocal cues with rich details in acoustic properties might be beneficial for investigating various types of positive emotions which were proposed to be primarily delivered via vocal-auditory channels (Scott, 2013). Distinct from other positive emotional sounds (i.e., cheering or relief), laughter can be composed of voiced and/or unvoiced segments making it a continuous but also chopping vocalisation by exhaled and inhaled breath; laughter can also be relatively involuntary or uncontrolled depending on the degree of expressed joyfulness and the context. Laughter is generated by repeated contraction of the diaphragm and intercostal muscles as it is characterised by spasmodic articulation which can also be seen as a modified way of breathing (Kohler, 2008; Provine, 2016; Scott, 2013).

Although quite distinct in emotional terms, crying is very similar to laughter in terms of production. The same vocal apparatus is found to underlie human vocal behaviour as in laughing, crying, speaking, singing, and other vocal expressions, but crying was observed to be especially similar to laughter compared to others – both vocalisations can be spasmodic, contagious, and involuntary. Crying sound has been described containing more sustained vowel-like voiced utterances, compared to laughter, and it also has a longer rhythmic pattern by having intervals synchronising with respiratory cycle (Provine, 2012). However, there has been somewhat less research into the vocalisations of crying, especially in adults.

### 1.3 The developmental and evolutionary perspective

#### *Crying*

Crying is the first recognisable emotional vocalisation that infants can produce to signal pain, hunger or fatigue, or to gain attention from caregivers, and is regarded as the primary emotional vocalisation to communicate infants' basic needs with their caregivers (Cohen-Bendahan, van Doornen, & de Weerth, 2014).

It has been reported that more than a single meaning in a class of emotional vocalisations is first observed in infants' crying sounds. Although cries of distress are only recognisable in babies older than six weeks (Bridges, 1932), it still remains to be investigated whether the crying of infants under a month is an emotional reaction or just part of general reactions (e.g., grabbing, kicking) due to excitement. However, empirical research has determined that there are different kinds of infant crying, which listeners can distinguish, including 'painful cry sounds' which have different average fundamental frequencies (F0) compared to 'growing discomfort cry sounds' (Green, Gustafson, Irwin, Kalinowski, & Wood, 1995). The painful cry sound is specific to sudden intense distress, while the 'growing discomfort cry sounds' are specific to the sensation of hunger, sleepiness, or tiredness. The painful cry sounds are perceived by adult participants as having decreasing urgency over time, while the hungry cry sounds are perceived as having increasing urgency over time. Over time, the average fundamental frequencies were consistently found to rise for hungry crying sounds and to fall over time for painful crying sounds (Zeskind, Sale, Maio, Huntington, & Weiseman, 1985). The difference between the perception of these two types of sounds is further demonstrated to be more dependent on duration and contexts but less on F0 (Zeifman, 2004), showing that these two types of crying sounds can reliably convey distinct needs to caregivers for establishing reciprocal relationship between infants and the surrounding environment in early stages.

Infants use crying sounds to signal their needs to caregivers, but they also use crying sounds to respond to cries of other infants. Calm infants started crying when they heard crying recordings of other infants, and crying infants continued crying when they heard cries of other infants but stopped when they heard their own crying sounds in the recordings (Martin & Clark, 1982). The results indicated that infants younger than 40 hours can distinguish their own crying from others, and furthermore, the 'contagious crying phenomenon' could be shown by only listening to recordings of other infants' cries. However, is this contagious crying phenomenon 'style specific'? When one-to-nine-month-old infants heard different styles of infant crying, such as intense distressed cries (i.e., the sudden sensation of pain), they would produce a similar pattern of distressed cry. There were not responding distressed crying sounds when the infants heard other styles of cries such as low intensity cries (e.g., the sensation of hunger)

(Geangu, Benga, Stahl, & Striano, 2010). This contagious crying response shows that crying can be a social response to others that specific behaviour is induced by another specific behaviour reliably. By producing the same style of crying when infants hear others, contagious crying is suggested to be an early sign of empathy development where infants share a similar affective state with others (Geangu et al., 2010).

However, the contagious crying phenomenon can be affected when feedback from the environment to crying infants is diminished. A depressed caregiver can have less responsive behaviour towards a crying infant than does a non-depressed caregiver (Field, Diego, Hernandez-Reif, & Fernandez, 2007). The infant's ability to distinguish their own crying from others can be impaired when their main caregiver suffered from depression, and these infants were also less responsive to cries of others than infants of non-depressed mothers (Field et al., 2007). The study indicated that when a crying infant could not solicit proper attending behaviour from main caregivers, the development of their crying behaviour can be affected. This interactive relationship between crying infants and the caregivers can suggest that the crying behaviour is sensitively connected to the outside environment of the crying infants.

Crying is mostly regarded as an early communication development, and the interaction between main caregivers and infants as stated above particularly received much attention (Boukydis & Burgess, 1982; Franklin et al., 2014; Murray, 1979). It has been shown that patterns of crying sounds could be recognised by caregivers when achieving further reactions from feeding, calming, or diaper changing (Bell & Ainsworth, 1972; Murray, 1979). Crying continues to be a prominent way of communicating negative emotion during the preschool years, as children's linguistic ability is still developing. However, crying behaviour decreases sharply during the second year and continues to decrease throughout childhood (Provine, 2012), which may be due to the developing cognitive and affective abilities of recognising, expressing, and regulating emotions.

### *Laughter*

Laughter, in addition to crying, is another emotional vocalisation that can elicit responsive behaviour from caregivers during a human's formative period of life.

Laughter is first expressed around two to four months of age and increases in frequency over time (Provine, 2012). The amount of laughter infants used to respond to an act of agent was observed to increase from 10% to 43% within four to twelve months in infancy (Sroufe & Wunsch, 1972). Laughing develops later than crying in babies as a means of interaction with their environment, but it effectively signifies an engagement in behaviour by an acting agent, which may prolong the interaction between babies and the agent (Bridges, 1932; Ruch & Ekman, 2001; Sroufe & Wunsch, 1972). Previous research on the interaction between infants and their mothers showed that infants' laughter was mostly followed by mothers' laughter rather than mothers' laughter being followed by infants' laughter. In the second year, coactive laughter (their overlapping laughter duration) was found to increasingly occur more than it did during the first year (Nwokah, Dobrowolska, & Fogel, 1994). These observations may provide evidence that laughter not only reinforces engagement of the parent, it also builds intimacy between producers and receivers of the laughter.

As children grow older, there is more laughing but less crying in daily life. The decrease of crying and increase of laughing might be shaped by social interactions and living experience (Brackett, 1934). As adults, crying seems to be present only in the company of close family members and friends, indicating that the social function of crying is crucial but limited to intimate relationships (Provine, 2012). Comparing to crying, the occurrence of laughter can be found in almost every conversation and social interaction and conveys positive signals that enhance the relationship between laugher and the receiver (Scott, 2013). Laughter is described as a 'social glue' which maintains intergroup affiliations (McGettigan et al., 2015), as it is usually associated with agreement, bonding, appreciation, and gratitude (Weisfeld, 1993).

Laughter is the only vocally expressed **positive** emotion which has been established to be recognised cross culturally (Sauter et al., 2010). In this study, several vocal cues were first generated by the European native English speakers and by the Himba, which is a remote seminomadic society in northern Namibia having little contact with modern Western culture. These emotional vocalisations communicating different emotional information including anger, disgust, fear, achievement, amusement, sensual pleasure, relief, sadness, and surprise were then presented to the UK participants and the Himba. The results demonstrated that



the basic emotional vocalisations (i.e., fear, sadness, surprise, anger, amusement, and disgust) were accurately recognised by the participants in both cultures, and the laughter representing joy (i.e., amusement) was the only recognisable vocal cue among positive emotional expressions. Other positive vocal cues expressing emotions of relief, sensual pleasure, and achievement were only recognisable within each culture but were not cross-culturally identified (Sauter et al., 2010). The cross-cultural finding on the successfully bidirectional recognition of laughter provide empirical evidence that although laughter begins later than crying in human infancy, it can be emerged from evolutionary heritage (Ekman, 1992a).

Laughter is not exclusive to humans, as it has been observed in other mammals such as rats and chimpanzees (Davila-Ross, Allcock, Thomas, & Bard, 2011; Panksepp, 2000, 2005; Panksepp & Burgdorf, 1999, 2003; Ross, Owren, & Zimmermann, 2009, 2010). Panksepp and Burgdorf (1999) reported that rats produced high frequency ultrasonic vocalisations (i.e., 50k-Hz chirps) when they were tickled by experimenters, in which the chirps were identified to resemble what the rats vocalised during social play signifying desire of social interaction (Knutson, Burgdorf, & Panksepp, 1998). The manual tickling by experimenters was further revealed to be an effective stimulation to induce positive affective states in rodents by showing reward-seeking behaviour (Knutson, Burgdorf, & Panksepp, 2002; Panksepp & Burgdorf, 1999). It is concluded that in contrast to other kinds of vocalisations with long length and low frequency range signifying aversive affective states, the kind of vocalisations with short length and high frequency range observed in young rats demonstrated an ancestral form of the human laughter which can be observed extensively during social play in human childhood (Panksepp, 2005).

In great apes, play panting is often observed during social playing, which can be spontaneously generated or as a response to play panting emitted by another social partner. In some occasions, play panting can occur by being tickled or during chasing (Davila-Ross et al., 2011; Matsusaka, 2004; Ross et al., 2009, 2010). Play panting was found to appear to prolong 'fragile' social playing, as one play partner continued performing aggressive behaviour and the play panting vocaliser used this kind of specific panting to encourage positive social interactions (Matsusaka, 2004). Play panting was found to be expressed

distinctively to serve different purposes (Davila-Ross et al., 2011). The expressions were distinguished depending on whether the play pants were spontaneously generated or socially elicited. In the latter situation, chimpanzees produced play panting to respond to the panting emitted by social partners. Just as one function of laughter in human society has been suggested to be social bonding, panting in chimpanzee colonies shares a striking similarity to human laughter in that it can signify cooperation and social affiliation. For example, new colonies produced more socially elicited panting than old colonies, and in contrast, old colonies produced more spontaneous panting than new colonies. Furthermore, old colonies produced significantly more spontaneous panting compared to socially elicited panting, while on the other hand, no significant difference was found in new colonies in terms of producing different kinds of panting. The socially elicited panting was found to be distinctively shorter than spontaneous panting, and the playing duration was reported to be maintained longer when there was more socially elicited panting involved. The authors suggested that the socially elicited panting resembles conversational laughter of humans, which encourages social interaction and establishes mutual affiliation (Davila-Ross et al., 2011).

## 1.4 Perceiving emotional information in social contexts

### 1.4.1 Appraisal theory and social norm

Perceiving emotional information can automatically elicit a process of evaluation in perceivers' minds (Moors, Ellsworth, Scherer, & Frijda, 2013). The process is proposed as a series of appraisal which directs perceivers to prepare appropriate reactions to emotional stimuli (Scherer, 2001). According to Scherer's appraisal theory (2001), perceivers consciously or unconsciously appraise emotional stimuli on the basis of relevance, implications, coping potential and normative significance. It states that perceivers constantly process external or internal events to evaluate their relevance and whether they deserve to be further processed; perceivers assess possible implications which can be caused by emotional stimuli and assess the extent to which affect the perceivers' survival in an uncertain environment; perceivers determine what types of responses are available under

different situations to coping with emotional stimuli; perceivers evaluate external and internal standards based on social or cultural norms related to emotional stimuli, and then determine an appropriate emotional reaction. The appraisal theory suggests that an emotional reaction is not merely a certain response corresponding to a certain stimulus, but a process depending on perceivers' personal experience, self-concepts, and social rules which perceivers valued (Ellsworth & Scherer, 2003).

Emotional expressions are delivered and received when both senders and receivers follow 'display rules' embedded in social norms (Ekman & Friesen, 1975). Social norms which govern how, when and what emotions individuals should express (Ekman, 2003). To acquire knowledge of display rules, individuals need to firstly be able to 'read' emotions beyond appearance. Pre-schoolers are found to be able to distinguish real (internal) emotions from apparent emotions expressed by adults, showing that 3- to 5-year-old children are developing abilities to understand that the meaning of emotional expressions are dependent on social contexts (Banerjee, 1997). The ability to recognise emotions which are socially contextualised keeps developing during adolescence (Blakemore, 2008). By developing social cognitive abilities, adolescents are building up competence of understanding others' emotions during complex social situations (Burnett & Blakemore, 2009). Simultaneously, adolescents are undergoing structural and functional brain development which can result in hypersensitivity to peer influence (Ahmed, Bittencourt-Hewitt, & Sebastian, 2015) and vulnerability to social rejection (Sebastian et al., 2011). These ongoing changes are suggested to contribute to adolescents' impulsive behaviour in which adolescents intend to follow group norms for obtaining peers' in-group approval (Burnett, Sebastian, Cohen Kadosh, & Blakemore, 2011). Recognising emotions and learning an appropriate reaction to an emotional event under various social contexts play central roles in human life.

Laughter and crying are social emotions constrained by emotional display rules built in cultures. For example, although laughter is mostly observed in social interactions, showing affiliations and affection between group members (Scott, Lavan, Chen, & McGettigan, 2014), laughter can also signal disapproval, schadenfreude, or taunting depending on distinct social contexts. On the other hand, crying can be a strong negative emotional expression signalling distress and

sadness, but it can also be used as an expression of joyfulness (e.g., winning a gold medal in tennis matches). Humans so far are the only animals to our knowledge who shed emotional tears (Provine, 2012), however the frequency of shedding tears is found to be associated with cultural differences. Specifically, a culture which is more open to self-disclosure and less restrict to display rules is more likely allowing individuals to shed emotional tears (van Hemert, van de Vijver, & Vingerhoets, 2011). Shedding tears can also induce complex emotional reactions in receivers who can be willing to help and feeling more connected to the tearful individual but also perceive them as less competent (van de Ven, Meijs, & Vingerhoets, 2017; Vingerhoets, van de Ven, & van der Velden, 2016). This complex emotional reaction toward tearful individuals can reflect appraisal process in perceivers' minds including whether the situation is relevant enough for further actions or whether the weeping behaviour violates display rules in a culture (Vingerhoets, Cornelius, Van Heck, & Becht, 2000).

#### 1.4.2 Theory of mind

Theory of mind is the ability to infer other's mental states and this mentalising ability is proposed to be a crucial psychological process underlying social interactions, as it enables individuals to interpret perceived emotions, intentions, behaviour, etc. Saxe and Kanwisher (2003) conducted an experiment investigating neural substrates activated in the process of reasoning others' minds. The study found robust and reliable brain activation in the temporoparietal conjunction (TPJ) that is selectively response to mentalising another human's mental state under social contexts, compared with reasoning nonhuman objects or reasoning another human's mind under non-social situations.

It is suggested that there is a partially overlapping relationship between emotion perception and the ability of reasoning others' mental states (Mitchell & Phillips, 2015). Perceiving emotions is proposed to involve a lower-level emotional information processing, and reasoning others' mind involves a higher-level cognitive processing. When perceivers need to decode social meanings of a complex emotional expression (e.g., sarcasm), the two processes converge to subserve a multi-level processing of information about people. Although some models (e.g., information processing approach) view emotion perception as a

precedent for mentalising other's emotional and intentional states (Corrigan, 1997), it is argued that they share common components (Mitchell & Phillips, 2015). There are also several candidate brain areas suggested to play roles in the overlapping relationship including medial and lateral prefrontal cortex, temporal pole, and TPJ (Frith & Frith, 2006; Hervé, Razafimandimby, Jobard, & Tzourio-Mazoyer, 2013; Mitchell & Phillips, 2015).

### 1.5 Functional neural imaging studies of laughter and crying

Only a few studies have investigated neural correlates underlying the production of laughter, and yet no studies to our knowledge have investigated the neural activations during the production of crying by healthy adults. For the investigation of producing laughter, Wattendorf et al. (2013) conducted a functional imaging study while participants laughed in the scanner. During tickling conditions, the participants were either instructed to inhibit laughter or to allow laughter during tickling. In further conditions the participants were instructed to produce laughter voluntarily without being tickled. There were highly similar regions identified in producing tickling laughter and voluntary laughter. However, when the participants inhibited laughter, the degree of involvement of lateral sensorimotor regions was greater than in the conditions when participants were allowed to burst into laughter or to laugh voluntarily. Moreover, in the same study the engagement of the lateral sensorimotor cortices was also shown when producing voluntary laughter and tickling laughter. The role of the lateral sensorimotor system is proposed to be involved in the production of laughter and in the inhibition of uncontrolled laughter.

In the neural correlates of laughter production demonstrated by Wattendorf et al. (2013), the lateral hypothalamus, parietal operculum, the amygdala, and right cerebellum increased activity during producing tickling laughter compared with producing voluntary laughter. Furthermore, activation of the periaqueductal gray matter (PAG) was observed during voluntary and tickling laughter but was absent during the condition of inhibiting laughter, thus the PAG area is proposed to act as a coordinating centre in the process of producing laughter.

Aside from tickling laughter and voluntary laughter, laughter has been suggested to have different types of expressions which can be correctly recognised by perceivers (Szameitat et al., 2009). The perception of tickling and other types of laughter (i.e., taunting and schadenfreude) was found to activate partly distinct brain regions, in which the right STG was suggested to be modulated by complex acoustic properties of tickling laughter, and the anterior rostral medial frontal cortex (arMFC) was proposed to be sensitive to other types of laughter associated with social saliency (Szameitat et al., 2010).

Gervais and Wilson (2005) suggested that there are two different kinds of laughter derived from biological and evolutionary basis: involuntary laughter, which is described to be spontaneous and automatic, and voluntary laughter, which is depicted as a volitional vocalisation mostly appearing in the context of social play. In a recent review, laughter is evidently shown as a complex vocal cue which is distinct from speech by having rapidly intercostal muscle movements and minimal supra-laryngeal modulation. On the other hand, laughter signals emotional intensity conveyed by the degree of its voluntary control, and listeners can decode different degree of involuntariness by either engaging in the similar emotional experience or by inferring mental states of others during social interaction (Scott, Lavan, Chen, & McGettigan, 2014).

Vocal crying in adults has received little attention in the research field. Although vocal laughing and crying develop from early infancy and both vocalisations preserve some degree of contagiousness, the frequency of vocal crying decreases with age and is replaced by tearful faces for expressing sadness (Provine, 2012). Crying behaviour in adults is observed to occur much less than laughing, however it is a prominent behaviour for soliciting assistance and to elicit perceivers' prosocial behaviour (Hendriks et al., 2008; Provine, 2012; Vingerhoets & Bylsma, 2016). Studies have shown that perceivers rated tearful faces as warmer but less competent (van de Ven et al., 2017), and crying faces were perceived as less aggressive and less emotionally stable compared to other expressions such as angry and fearful faces (Hendriks & Vingerhoets, 2006).

A study discovered that when authentic laughter and crying sounds accompanied by emotional facial expressions were simultaneously shown to participants, the information of facial expressions was automatically integrated in

the process of evaluation even though they were requested to evaluate the valence of the vocalisations (Lavan, Lima, Harvey, Scott, & McGettigan, 2015). The underlying neural correlates of perceiving laughter and crying was reported that the auditory cortex, amygdala, and insula were more active in perceiving laughter and crying compared with perceiving the same vocalisations but in a time-reversed form (Sander & Scheich, 2001, 2005).

Although neuroimaging studies investigating laughter and crying in healthy adults are relatively rare, it is worth noting that these two vocalisations have been studied in patients from the last century. More literature will be reviewed in the next sections.

## 1.6 Neurobiology of pathological laughing and crying

### 1.6.1 Pathological laughing and crying

Both laughter and crying are—uniquely—associated with clinical, pathological production disorders, in which they are produced in an uncontrolled and inappropriate fashion. Other non-verbal emotional expressions (e.g., disgust, fear) are not frequently described in conditions where their production is inappropriate or uncontrolled. In pathological laughter and crying, which can occur separately or together, the production is inappropriate, involuntary, and may or may not be linked to affective states.

Pathological laughing and crying (PLC) is a symptom of involuntary emotional expression disorder (IEED), in which patients express disproportionate or inappropriate laughter and/or crying in response to evoking stimuli. Wilson (1924) first described PLC as uncontrollable emotional displays which were dissociated from underlying mood. A model of emotional expression regulation which involved dual pathways for voluntary control and involuntary control was described to account for PLC. Voluntary control is associated with volitional motor pathways which allow voluntary emotional expressions, while involuntary control is driven by emotional motor pathways and can be inhibited by the voluntary pathway (Wilson, 1924). PLC is viewed to be abnormal function of a volitional motor pathway which disinhibits activities of emotional motor

pathways. The functions of these two pathways can be seen in cases of emotional facial paresis (EFP) and volitional facial paresis (VFP). EFP patients can express emotions voluntarily but cannot produce normal involuntary emotional expressions, such as not laughing when told a joke. In contrast, VFP is observable when a patient cannot express emotions when instructed, but their emotional expressions driven by involuntary emotional impulses are preserved. Both VFP and EFP patients have concurrent affective states that are consistent with the emotional stimuli, but only the EFP patients were unable to involuntarily express emotions. According to this theoretical model, when the volitional motor pathway is damaged, PLC patients would involuntarily express emotions which can be evoked by inciting stimuli regardless of consistency to the emotion, and they are unable to terminate the disproportionate or inappropriate expression.

A second subtype of IEED is known as emotional lability (EL), which had its first diagnostic criteria detailed by Cummings et al. (2006). Similar to PLC, EL patients suffer from disproportionate or inappropriate episodes of laughter and/or crying. However, the expressions are disproportionate to inciting stimuli. In contrast to PLC, EL patients express uncontrollable emotions *consistent with* underlying mood. However, although a considerable number of cases of PLC syndrome have been reported since 1924, terminological confusion is apparent in the literature between PLC and EL as IEED subtypes (Lauterbach, Cummings, & Kuppaswamy, 2013). In the paper by Lauterbach et al. (2013), 655 citations were found when researching IEED-related topics, and only 20 were specified with PLC, 35 with PL, and only 12 papers reported PC; the others incompletely specified the IEED subtypes.

In terms of the underlying neurobiology of IEED, a wide variety of brain lesions have been found to be associated with PLC (Lauterbach et al., 2013). Wilson (1924) outlined the difficulties of deciphering the underlying mechanism of PLC, “Hopeless as it is to disentangle specific mechanism from widespread disorders of function entailed by equally widespread lesions” (p. 319). In addition to Wilson’s nine cases, Lauterbach et al. (2013) thoroughly reviewed studies over the past decades and their results determined that PLC-associated widespread lesions can be found in various brain abnormalities, such as strokes, tumours (e.g., Achari & Colover, 1976), multiple sclerosis (MS) (e.g., Haiman, Pratt, & Miller, 2008), Parkinson’s disease (e.g., Petracca, Jorge, Acion, Weintraub,



& Robinson, 2009), and amyotrophic lateral sclerosis (ALS) (e.g., Gallagher, 1989). These lesions can be found in multiple brain regions and are also associated with degeneration of multiple brain functions, which further complicates any anatomic attribution.

However, despite the wide range of damaged brain areas observed in PLC patients, papers which specified PL, PC, or PLC may still guide our understanding of the differences/commonalities in the neural mechanisms that underlie the syndromes of pathological laughter and/or crying.

### 1.6.1.1 Neurodegenerative diseases

#### *Damage to central neural system*

Amyotrophic lateral sclerosis (ALS) and multiple sclerosis (MS) are neurodegenerative diseases which selectively affect central neural system function, and both diseases can be accompanied by PLC syndrome. ALS is a motor neurone disease which impacts the motor components of the spinal cord and bulbar areas (i.e., the midbrain, pons, medulla, cerebellum). This corticobulbar disease weakens the voluntary control of patients, and the prevalence of PLC is reported to be 49% of the ALS patient population (Lauterbach et al., 2013). Since ALS is an age-related disease, the cause of PLC has been related to the ageing brain (Gallagher, 1989). However, Gallagher (1989) concluded that the origin of PLC in ALS patients may be due to the bulbar palsy rather than due to solely age-related changes.

MS is also a neurodegenerative disease in which the corticospinal tract is mainly affected. By comparing lesion areas between MS patients with (n = 14) and without (n = 14) PLC syndrome who were all distinct from comorbid mood disorder, Ghaffar, Chamelian, and Feinstein (2008) identified neuroanatomical correlates of PLC which were damaged in MS-PLC patients but remained intact in the non-PLC MS patients. Discrete differences in lesion volume were noted in six brain areas: brainstem, bilateral medial inferior frontal areas, bilateral inferior parietal areas, and right superior medial frontal area (i.e., superomedial M1). The distinct distribution of lesions identified in MS-PLC from non-PLC MS implicates the association of a network of regions with PLC, which supports the bulbar involvement and the prefrontal dysfunction that were demonstrated in

ALS-PLC patients but not in non-PLC ALS patients. The PLC group and the non-PLC group both have damage to the corticospinal tract, however the MS patient who acquired PLC showed more lesions in the superomedial M1. The lesion in the parietal lobe is considered to be part of a putative neural network, which is a feedback loop running between the amygdala and medial inferior frontal regions. This circuit is proposed to mediate an involuntary component of emotional expressions, which receives input from primary sensory association areas in the parietal lobe and sends projections to the brainstem and hypothalamus (Mega, Cummings, Salloway, & Malloy, 1997).

MS and ALS patients were having impairments in the corticospinal and in the corticobulbar track respectively. These tracks both originate from the cerebral cortex including the primary motor cortex, premotor cortex, supplementary motor area, post central gyrus, and parietal cortex. The fibres of both tracks travel through the internal capsule, midbrain, pons, and then to the medulla. While the corticospinal track terminates at different levels of the spinal cord, the corticobulbar track terminates in the brainstem. Along these two tracks from cerebral motor areas to subcortical areas, not only ALS and MS patients were frequently found to have PLC syndrome, other lesions which include these areas can also be accompanied by PLC syndrome. For example, patients with lesions in the pons (Arif, Mohr, & Elkind, 2005; Elyas, Bulters, & Sparrow, 2011), midbrain, and cerebellum (Parvizi, Anderson, Martin, Damasio, & Damasio, 2001) were found to have PLC as secondary symptoms.

#### *Dysfunctions in prefrontal regions*

The presence of PLC in ALS and MS patients both appears to be associated with impairment in the functional integrity of the prefrontal cortex. McCullagh et al. (1999) used the Wisconsin Card Sort Test (WCST) to probe dorsolateral prefrontal function between ALS-PLC patients and ALS non-PLC patients regarding performance. Patients with PLC made significantly more total errors on the WCST than the other two groups, which suggested that besides the primary motor and its descending tract possibly contributing to the development of PLC syndrome, the dorsolateral prefrontal cortex dysfunction may also play a role.

The prefrontal dysfunction was also demonstrated to be involved in MS-PLC patients who performed worse than non-PLC MS patients on the Stroop Task and the Controlled Oral word Association Test (COWAT) (Feinstein, O'Connor, Gray, & Feinstein, 1999), and the significant difference further supports a possible relationship between the prefrontal function and PLC syndrome which was identified in the ALS patients. However, PLC and non-PLC MS patients did not perform differently on the Wisconsin Card Sort Test (WCST) which is also a typical test of the prefrontal function. The authors suggested that it is because the WCST although is sensitive to the prefrontal function, it is not a timed task. Patients with PLC appear to have relatively greater difficulties with speed of information processing than the non-PLC MS group. Because this slow cognitive processing is considered one of the hallmarks of subcortical dementia, the authors proposed that this is due to additional subcortical lesions. However, the plausibility of this proposed explanation is unable to be validated since the fMRI data is absent in the study.

### 1.6.2 Pathological laughing

The subcortical lesion areas observed in PLC literature greatly overlap with lesion areas in patients found to have selectively pathological laughing syndrome, such as the brainstem (e.g., Gallagher, 1989) and cerebellum (e.g., Parvizi & Schiffer, 2007). The internal capsule is a part of the corticobulbar tract where the tract descends through it to the midbrain, and when the internal capsule was damaged, patients were found to have *31aemoglo prodromique*—crazy/forced laughter—in many cases (e.g., Ceccaldi & Milandre, 1994). The pulvinar and thalamic nuclei was another brain site which, when damaged, patients were found to have pathological laughing (e.g., Lauterbach, Price, Spears, Jackson, & Kirsh, 1994).

Patients reported to have more cortical lesions are more likely to develop pathological laughing rather than PLC. Mendez, Nakawatase, and Brown (1999) reported a patient with lesions in bilateral orbitofrontal areas and anterior cingulate gyrus who suffered from PL for 20 years. Tsutsumi, Yasumoto, and Ito (2008) reported a patient with a tumour in the right frontal lobe involving premotor cortex, who developed PL three months after the onset of hemiparesis. After surgery, the PL syndrome disappeared. In this case, the brainstem,

thalamus, hypothalamus, cerebellum, and internal capsule were undamaged. Schmitt et al. (2006) stimulated the supplementary sensorimotor area and lateral premotor cortex in two patients for pre-surgical epilepsy evaluation and reported that laughter was generated in absence of emotional content.

Wilson (1924) proposed that the origin of the anterior corticospinal tract, from the frontal operculum and lower end of the precentral gyrus, is considered as a 'voluntary control centre' of emotional expression. Furthermore, PLC syndrome was suggested to occur when the descending pathway from the frontal operculum to the cerebellum and to the basis pontis was disrupted (Parvizi et al., 2001). However, the exact role of the frontal areas in the PLC mechanism remains unclear. Previous studies showed that PLC patients had more difficulties than non-PLC patients in performing the cognitive tasks which are sensitive to prefrontal function, and the lesions in the frontal lobe and the spheromedial M1 were more severe in the MS-PLC group than in the non-PLC MS group. Furthermore, the focal frontal lesions can be found in the patients who selectively acquired pathological laughing, suggesting that the region may play a specific role in generating laughter.

### 1.6.3 Pathological crying

A more limited network of subcortical regions is associated with pathological crying. Pathological crying has been observed in patients with lesions in the brainstem (e.g., Andersen, Ingeman-Nielsen, Vestergaard, & Riis, 1994), internal capsule (Bharathi & Lee, 2006), midline cerebellar cyst (Parvizi & Schiffer, 2007), and bulbar components (Gallagher, 1989) and has been observed in patients with diseases such as Parkinson's disease (Petracca et al., 2009) and Machado-Joseph disease (Guimarães, Bugalho, & Coutinho, 2008).

Parkinson's disease (PD), as a degenerative disorder of the central nervous system, mainly affects the motor system. Petracca et al. (2009) investigated 131 PD patients and found 22 with pathological crying and 15.3% comorbid with depression. In addition, not only PC syndrome was identified in PD patients, but also the syndrome was found to be associated with the severity of PD. However, the anatomic attributions of PC were difficult to identify in PD patients due to multiple damaged regions.

The Pathological crying was also shown when the patient had been deeply stimulated in the subthalamic-thalamic region (Okun et al., 2004) and the internal capsule (Low, Sayer, & Honey, 2008). So far from the literature, PC is very different from the PLC and PL syndromes, in which the latter two syndromes were reported with a wide variety of lesions in the cortical and/or subcortical areas.

#### 1.6.4 Gelastic and dacrystic seizures

Gelastic (laughing) and dacrystic (crying) seizures are rare types of epileptic syndromes and frequently reported when patients have hypothalamic hamartomas (HH) (Kahane, Ryvlin, Hoffmann, Minotti, & Benabid, 2003). These patients suffer from laughter (i.e., gelastic) and/or crying (i.e., dacrystic) attacks for seconds to a minute once or several times a day without accompanying mirth or sadness. HH are rare tumour-like developmental malformations which occur in the region of the inferior hypothalamus, which is suggested to play a crucial role in the gelastic and dacrystic seizures. When the HH was removed from patients, they were reported to be seizure free after surgery (Kahane et al., 2003). Kahane et al. (2003) investigated five patients with gelastic and/or dacrystic seizures associated with HH, and four of the five patients were recorded using stereotactic intracerebral EEG (SEEG) during seizures. After the HH discharges, these recordings also showed subtle cortical EEG changes recorded over the two cingulate gyri (gelastic), the right fronto-centro-temporal regions (dacrystic), and the right orbito-cingulate cortex (mixed). In contrast, the recordings of the fourth patients (gelastic) were mainly observed to occur at the cortical level (i.e., the left cingulate gyrus and the left hippocampus), whereas the changes recorded in the HH were subtle. The authors suggested that the cortical EEG changes were due to a spread of seizure activity from the HH to the cortex, regardless of the epileptic types (gelastic or dacrystic seizures). The evidence so far indicated that the hypothalamus is highly associated with gelastic and/or dacrystic seizures. However, there might be a closer relationship between HH and gelastic/dacrystic seizures (Parvizi et al., 2011) than the relationship between HH and pure dacrystic seizures (Blumberg et al., 2012).

Parvizi et al. (2011) reviewed 100 patients with HH and gelastic seizures. The lesion sites in all patients were confined to mammillary bodies in the posterior hypothalamus. 32 of the 100 patients with pure gelastic seizures had longer durations of epilepsy than the rest of the patients who had multiple types of seizure. In the review, no dacrystic seizure was mentioned. However, the limited presence of dacrystic seizures may be due to the intrinsically scarce number of cases. Blumberg et al. (2012) reviewed 6851 patients admitted to EEG long-term monitoring studies (i.e., at least 12 hours) in five epilepsy centres. The authors found nine cases with dacrystic seizures which resulted in a 0.13% frequency of dacrystic seizures, and even when the authors included patients reported to have dacrystic seizures since 1990, the frequency was still considered to be low (i.e., <0.5%). In the nine cases the authors reviewed, five patients with gelastic and dacrystic seizures were all found to be associated with HH, however three of the four patients with pure dacrystic seizures were found to have mesial temporal sclerosis (MTS). The fourth dacrystic patient was found to have left frontal glioblastoma. Although the HH and MTS were both reported to be common substrates underlying dacrystic seizures (Tatum & Loddenkemper, 2010), mesial temporal regions seem more likely to be associated with the pure dacrystic seizures.

In conclusion, few points can be addressed from the review of comparing the neural substrates underlying the PLC, PL, and PC. Firstly, damage to the corticobulbar and the corticospinal tracts accompanying by the dysfunction in the prefrontal regions can likely lead to PLC syndrome, rather than to the pure form of PL or PC. Secondly, PL seems to show well localised areas in the M1 and frontal regions associated with the syndrome. Thirdly, cases of PC are the rarest found in the IEED syndrome, in addition the PC has more opportunities to be found in patients identified only with damages to the subcortical regions. However, PC as the rarest case reported, which can be due to the syndrome is likely closely linked to emotional liability, so complicated PC cases were excluded from our review. Finally, patients with epileptic seizures can be found other cortical regions showing abnormal neural activities which were infrequent identified in other kinds of patients (e.g., MS, ALS).

Although the current experiments in this thesis only focus on the perception of laughter and crying, the knowledge of similarities and

dissimilarities reviewed on the patient studies can pinpoint the possible areas which are highly associated with the perception of laughter and crying. Moreover, it can provide beneficial information to understand the underlying mechanism of involuntary and voluntary pathways.

## Chapter 2 Aims of the thesis

The aims of the thesis are to explore underlying processes involved in the perception of laughter and crying, and to determine whether similar psychological processes are involved in perceiving laughter and in perceiving crying, and how this is affected by differences between involuntary and voluntary vocalisations. There are three distinct approaches used in this thesis: behavioural rating tasks, physiological responses recordings, and neuroimaging techniques.

The first experiment took place at the Science Museum in London. By collecting behavioural data from a large number of participants with various backgrounds and ages, we aim to find out developmental trajectories of perceiving these emotional vocalisations (see Chapter 4).

The second experiment used pupillometry to understand the physiological responses to these emotional vocalisations, in which the technique can provide us a continuous index of the perception with high temporal resolution measure of the underlying biological changes (see Chapter 5).

The third experiment used neuroimaging technique to further investigate the neural correlates underlying the perception of laughter and crying, and we aim to understand the inconsistent results derived from the behavioural rating tasks and the physiological response recordings (see Chapter 6).



## Chapter 3 Materials preparation

### 3.1 Emotional stimuli

We recorded voluntary and involuntary exemplars of laughter and crying from six adults who were not professional actors (aged between 23 to 46 years; three females). Recordings were generated in a sound-proof, anechoic chamber at University College London. Stimuli were recorded with a Bruel Kjaer 2231 Sound Level Meter on a digital audio tape recorder (Sony 60ES; Sony UK Limited, Weybridge, UK) and fed to the S/PDIF digital input of a PC sound card (M-Audio Delta 66; M-Audio, Iver Heath, UK). Speakers were always asked to produce voluntary vocalizations before involuntary vocalisations. This practice aimed to avoid any effect of the emotional states associated with involuntary vocalisations on the production of voluntary vocalisations. To produce voluntary vocalisations, speakers were asked to generate vocalisations without external stimulation and in the absence of an underlying emotional state. The procedures for involuntary laughter and involuntary crying were different. To elicit involuntary laughter, each speaker was shown funny videos on a computer screen and with headphones, using videos that were previously identified as amusing by the speakers (Lavan et al., 2015; McGettigan et al., 2015). The participants described the emotional experience during and after the recording session of involuntary laughter as delightful and each participant confirmed that they had been laughing spontaneously. Because it is difficult to create an experimental situation that would induce an emotional state of sadness for all participants, speakers were asked to think about negative events (i.e., personal loss or tragedy) that could induce a sad mood in order to evoke involuntary crying. As a result of this negative emotional experience by self-induction, speakers reported feeling sorrowful and sad. Recording sessions lasted around one hour per speaker.

The raw audio files were downsampled at a rate of 44100 Hz to mono.wav files with 32-bit resolution. Individual files were prepared for each vocalisation from each speaker by visually identifying the onset and offset of each event in the oscillograms. All files were then normalised for root-mean-square (RMS) amplitude using PRAAT (Boersma & Weenink, 2015). Fifty tokens were extracted per category (200 in total) and submitted to pilot perceptual validation (average duration = 2.51 seconds; SD = 0.36; range = 1.7 – 3.14).

Thirty native British speakers took part in the pilot experiment (average age = 24.93 years; SD = 4.77; range = 19 – 38; 16 females; none of these participants took part in the main study). They were asked to rate each of the 200 stimuli on four different parameters using the following 7-point Likert scales: authenticity, emotion, and control. These rating scales corresponded to separate blocks, and the order of the blocks was counterbalanced across participants. For authenticity ratings, participants rated the extent to which the emotional sound reflected a genuinely-felt emotion ('Does the sound reflect a genuinely-felt emotion?' 1 signified posed: the speaker was not feeling the emotion and 7 signified genuine: the speaker was genuinely feeling the emotion). Participants were informed that half of the sounds were genuine and half were posed. For emotion ratings, participants rated the extent to which the emotional sound expressed happiness or sadness ('Does the sound express happiness or sadness?' 1 signified that the person was very sad, and 7 signified that the person was very happy). For frequency ratings, participants rated the extent to which the emotional sounds are heard in everyday life ('How frequently do you hear these sounds in your everyday life?' 1 signified very rarely, and 7 signified very often). Finally, for control ratings, participants rated the extent to which the speaker could control the vocalisation or not ('Can the speaker control the expression?' 1 signified that the speaker was in control while 7 signified that the speaker was not in control). Although response latencies were not measured, participants were encouraged to be as quick as possible; they had up to three seconds to respond after the stimulus' offset. The order of stimuli was randomized in each block and responses were collected via keyboard presses. Stimuli were presented using laptops with MATLAB (version R2012b, Mathworks, Sherborn, MA, USA) and the psychophysics toolbox (Brainard 1997; Pelli 1997), and played via high-quality headphones (Sennheiser Professional HD 25-II).

A 2x2 ANOVA was conducted for each scale, with expression (laughter/crying) and involuntariness (involuntary/voluntary) as repeated-measures factors. On the authenticity scale, involuntary vocalisations ( $M = 4.58$ ,  $SD = 0.67$ ) were rated higher (i.e., more authentic) than voluntary vocalisations ( $M = 3.31$ ,  $SD = 0.45$ ; main effect of involuntariness:  $F[1,29] = 102.257$ ,  $MSE = .47$ ,  $p < .001$ ,  $\eta_p^2 = .779$ ). The main effect of expression was also significant, indicating that laughter ( $M = 4.48$ ,  $SD = 0.53$ ) was generally rated as more authentic than crying ( $M = 3.42$ ,  $SD = 0.72$ ;  $F[1, 29] = 41.971$ ,  $MSE = .801$ ,  $p < 0.001$ ,  $\eta_p^2 = .591$ ). The interaction was also significant ( $F[1, 29] = 32.353$ ,  $MSE = .184$ ,  $p < 0.001$ ,  $\eta_p^2 = .527$ ), indicating that the difference between involuntary crying and voluntary crying in perception of authenticity was smaller than the difference between involuntary laughter and voluntary laughter. A follow up pairwise comparison was conducted for each expression to test whether the authenticity ratings of involuntary vocalisations differed from voluntary vocalisations. Involuntary laughter ( $M = 5.33$ ,  $SD = 0.72$ ) was rated higher than voluntary laughter ( $M = 3.62$ ,  $SD = 0.78$ ;  $t(29) = 8.91$ ,  $p < .001$ ), and involuntary crying ( $M = 3.82$ ;  $SD = 0.80$ ) was rated higher than voluntary crying ( $M = 3.00$ ;  $SD = 0.72$ ;  $t(29) = 10.08$ ,  $p < .001$ ) (Fig. 3.1).

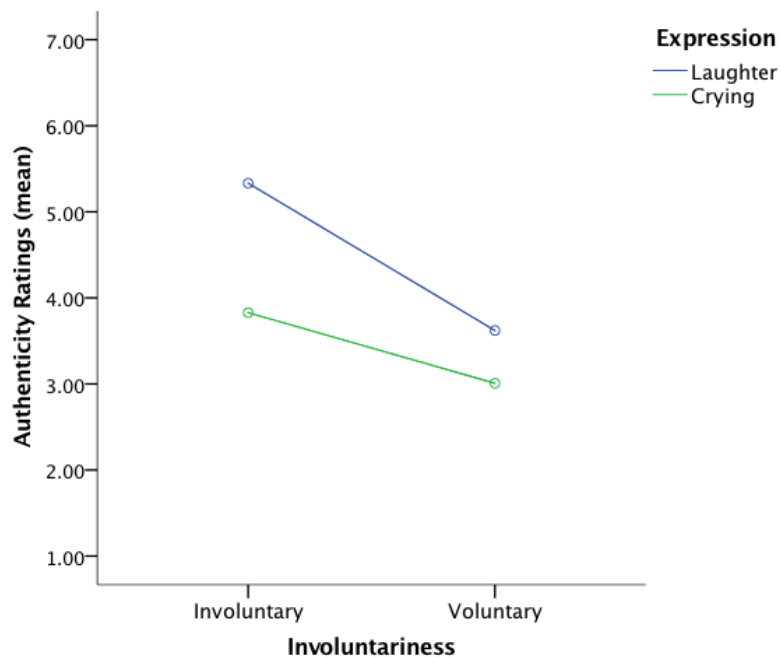


Figure 3.1 Authenticity ratings of the four conditions

On the emotion scale, laughter ( $M = 5.59$ ,  $SD = 0.48$ ) was generally rated more positively than crying ( $M = 2.42$ ,  $SD = 0.40$ ), as expected (main effect of expression:  $F[1,29] = 612.001$ ,  $MSE = 301.470$ ,  $p < .001$ ,  $\eta_p^2 = .955$ ). Involuntary expressions ( $M = 4.21$ ,  $SD = 0.35$ ) were also rated more positively than voluntary expressions ( $M = 3.81$ ,  $SD = 0.25$ ; main effect of involuntariness:  $F[1,29] = 69.986$ ,  $MSE = 4.956$ ,  $p < .001$ ,  $\eta_p^2 = .707$ ). A significant interaction ( $F[1,29] = 40.919$ ,  $MSE = 3.942$ ,  $p < .001$ ,  $\eta_p^2 = .585$ ) suggests that involuntary laughter ( $M = 5.98$ ,  $SD = 0.54$ ) was perceived more positively than voluntary laughter ( $M = 5.21$ ,  $SD = 0.53$ ;  $t(29) = 9.497$ ,  $p < .001$ ), while there was no difference between involuntary crying ( $M = 2.45$ ,  $SD = 0.42$ ) and voluntary crying ( $M = 2.40$ ,  $SD = 0.46$ ;  $t(29) = .649$ ,  $p = .522$ ) (Fig. 3.2).

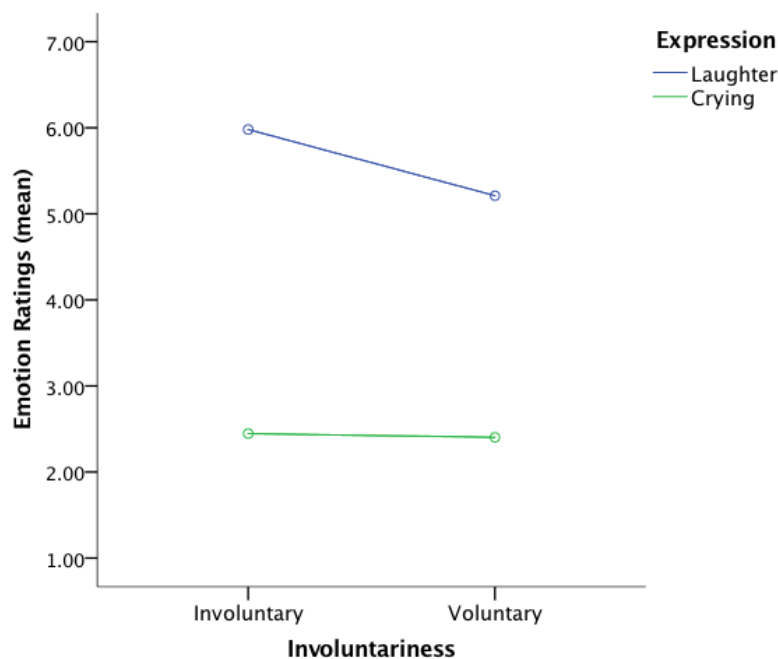


Figure 3.2 Emotion ratings of the four conditions.

On the frequency scale, only the main effect of expression was found significant; that is, laughter ( $M = 4.45$ ,  $SD = 0.90$ ) was reported to be heard more often in everyday life than crying ( $M = 2.08$ ,  $SD = 0.62$ ;  $F[1,29] = 161.951$ ,  $MSE = 1.039$ ,  $p < .001$ ,  $\eta_p^2 = .848$ ). The main effect of involuntariness was found not

significant on the frequency scale, which suggests that involuntary vocalisations (M = 3.34, SD = 0.65; involuntary laughter: M = 4.48, SD = 0.95; involuntary crying: M = 2.21, SD = 0.63) were not heard more frequently than voluntary vocalisations (M = 3.19, SD = 0.64; voluntary laughter: M = 4.43, SD = 1.10 ; voluntary crying: M = 1.96, SD = 0.64;  $F[1,29] = 2.245$ ,  $MSE = .710$ ,  $p = .145$ ,  $\eta_p^2 = .072$ ). There was also no significant interaction between expression and involuntariness ( $F[1,29] = 1.471$ ,  $MSE = .320$ ,  $p = .235$ ,  $\eta_p^2 = .048$ ) (Fig. 3.3).

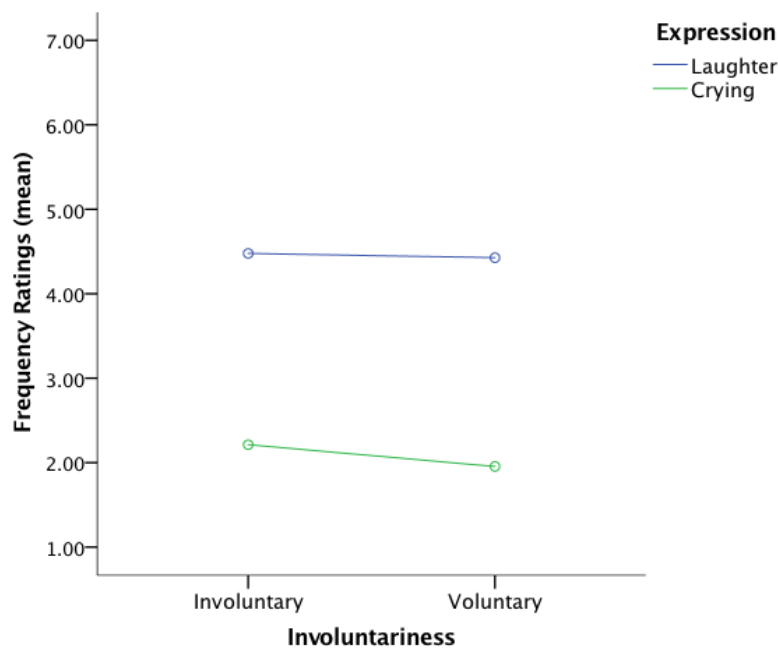


Figure 3.3 Frequency ratings of the four conditions

Finally, on the control scale, involuntary vocalisations (M = 5.02, SD = 0.58) were rated as sounding like the speakers were in control of the expression voluntary vocalisations (M = 3.61, SD = 0.44; main effect of involuntariness,  $F[1,29] = 184.320$ ,  $MSE = 60.080$ ,  $p < .001$ ,  $\eta_p^2 = .864$ ). The main effect of expression was not significant (laughter: M = 4.43, SD = 0.42; crying: M = 4.20, SD = 0.76;  $F[1,29] = 2.059$ ,  $MSE = 1.553$ ,  $p = .162$ ,  $\eta_p^2 = .066$ ), which indicates that the participants perceived no difference between laughter and crying in terms of control or lack thereof by the speakers. However, a significant interaction ( $F[1,29] = 57.510$ ,  $MSE = 11.508$ ,  $p < .001$ ,  $\eta_p^2 = .751$ ) suggests that

the difference between involuntary laughter ( $M = 5.45$ ,  $SD = 0.60$ ) and voluntary laughter ( $M = 3.41$ ,  $SD = 0.61$ ;  $t(29) = 13.115$ ,  $p < .001$ ) was perceived as showing greater differences in speaker control than the difference between involuntary crying ( $M = 4.60$ ,  $SD = 0.81$ ) and voluntary crying ( $M = 3.80$ ,  $SD = 0.77$ ;  $t(29) = 9.923$ ,  $p < .001$ ) (Fig.3.4).

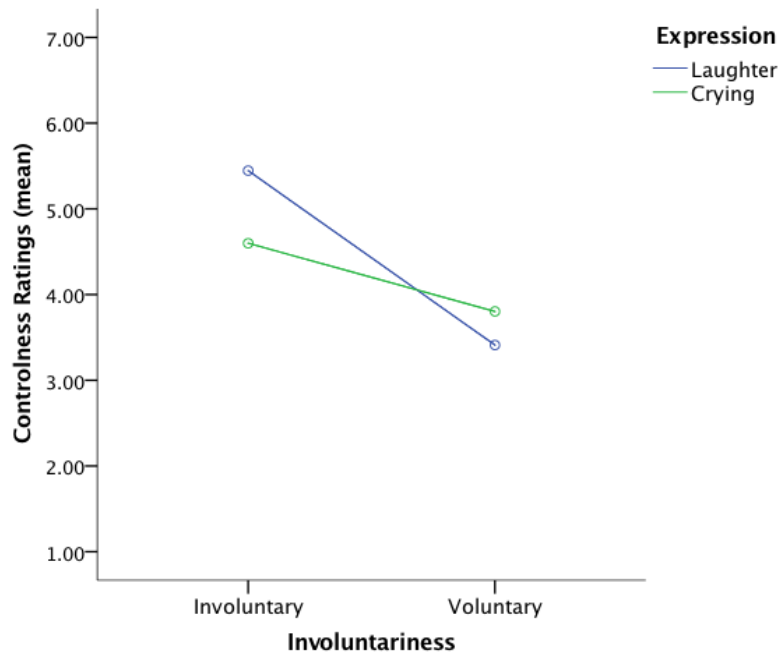


Figure 3.4 Control ratings on four conditions.

### 3.2 Main studies

For the following experiments, 20 tokens were selected for each condition from the pilot dataset (80 in total). For the involuntary laughter and involuntary crying conditions, we selected the most highly-rated tokens on the authenticity scale. All samples of involuntary laughter were rated above the mid-point of the scale (i.e., above four) ( $M = 5.80$ ;  $SD = 0.45$ ; range = 4.833 – 6.50) while the samples of involuntary crying were mostly rated above 4 (only three of 20 stimuli were

below four,  $M = 4.47$ ;  $SD = 0.47$ ; range = 3.885 – 5.310). These two groups of involuntary emotional vocalisations were rated differently based on the authenticity scale ( $t(38) = 9.134, p < .001$ ), which may reflect basic differences between these stimuli (Fig. 3.5). For the voluntary laughter and crying conditions, the tokens that received the lowest ratings on the authenticity scale were selected; they were all rated below the mid-point of the scale (i.e., below four) (laughter:  $M = 3.299, SD = 0.426, \text{range} = 2.433 - 3.933$ ; crying:  $M = 2.638, SD = 0.787, \text{range} = 1.033 - 3.900$ ). These two groups of voluntary tokens were also rated differently on the authenticity scale ( $t(38) = 3.295, p = .002$ ) (Fig. 3.5). In each condition, half of the tokens were produced by male speakers and half by female speakers. The stimuli were matched for duration across conditions (involuntary laughter:  $M = 2.530$  seconds,  $SD = .385$ ; voluntary laughter:  $M = 2.382$  seconds,  $SD = .362$ ; involuntary crying:  $M = 2.649$  seconds,  $SD = .265$ ; voluntary crying:  $M = 2.486, SD = .375$ ), and no significant difference in duration was found (main effect of expression:  $F[1,19] = 2.541, p = .127, \eta_p^2 = .118$ ; main effect of authenticity:  $F[1,19] = 3.107, p = .094, \eta_p^2 = .141$ ; interaction:  $F[1,19] = .015, p = .904, \eta_p^2 = .001$ ).

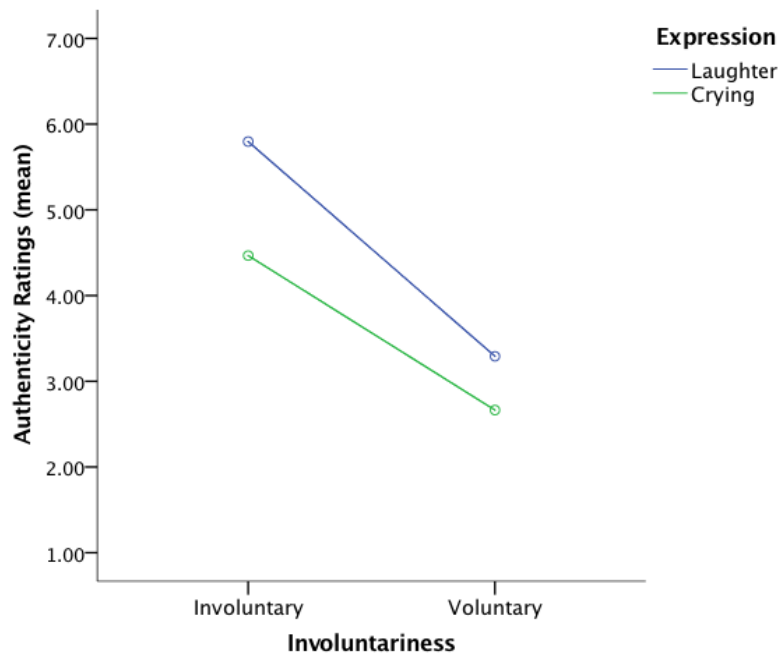


Figure 3.5 Authenticity ratings of the selected 80 stimuli

## Chapter 4 The Science Museum Project

### 4.1 Introduction

Over our life span, we experience different emotions and continuously change the way we express and respond to emotions. As we grow older, we learn to modulate the expression of our emotions according to the social context. Not only do our emotional expressions evolve, but we also learn to understand and react to the emotional vocalisations made by others.

The ability to recognise facial emotions develops early in life. During infancy, 4-month-old infants are able to distinguish smiling and frowning facial expressions (Barrera & Maurer, 1981). Hertenstein and Campos (2004) observed that the social behaviour of 14-month-old infants can be affected by facial expressions of disgust or happiness that adults exhibited one hour prior. Moreover, pupillary responses of 14-month-old infants increased more when they were viewing incongruent pairs of facial expressions and actions in adults than when they viewed congruent pairs (Hepach & Westermann, 2013). From the age of 3-to-5 years, preschool children continue to develop the ability to recognize facial emotional expressions until adolescence. According to previous research, preschool children recognise facial expressions with the lowest accuracy, compared to other groups. Among preschool children, school children, and young adolescents, accuracy increases by ascending age group. Young adolescents, however, do not perform differently to late adolescents (Herba, Landau, Russell, Ecker, & Phillips, 2006; Montirosso, Peverelli, Frigerio, Crespi, & Borgatti, 2010).

Although little research has focused on developmental trajectories of recognising vocal emotions, there is evidence that the ability develops from



infancy. At the age of seven months, infants can discriminate spoken words in happy and angry prosody from neutral prosody, which manifests in increased oxygenated 45aemoglobin concentration changes in the right hemisphere (Grossmann, Oberecker, Koch, & Friederici, 2010). At this age, they are also able to distinguish congruent pairs of vocal and facial emotional expressions by showing more centro-parietal positive component (~600 ms) for congruent pairs than for incongruent pairs (Grossmann, Striano, & Friederic, 2006). Furthermore, there is evidence that the ability to distinguish vocal emotional expressions continues to develop throughout childhood. At the age of 5-to-10-years, children can correctly match vocal emotional expressions to photographs of facial emotions, and this ability improves with age. Moreover, children are better at recognizing some vocal expressions (e.g., amusement, relief, and disgust) than others (e.g., sadness and neutral), indicating that the ability to recognise different vocal emotions may follow distinct developmental trajectories of emotion processing (Sauter, Panattoni, & Happé, 2013). The finding that children's ability to recognise vocal expressions of sadness develops more slowly than the ability to recognise other emotional expressions has been replicated by a recent study (Chronaki, Hadwin, Garner, Maurage, & Sonuga-Barke, 2014). In this study, non-linguistic vocal expressions were generally recognised less accurately than facial expressions. In addition, the researchers found that the ability to recognise expressions of sadness continues to develop after the age of 11 years. The ability to recognise non-linguistic, emotional vocal expressions of sadness, therefore, is consistently reported to develop more slowly, and later, than the ability to recognise facial expressions of sadness or expressions of anger and happiness in both modalities.

Emotional development in adolescence is usually studied in regards to developmental changes in the brain. The starting point of adolescence is defined by the onset of puberty. Along with hormonal changes, adolescents are characterized during this transition period from childhood to adulthood by a tendency toward risk-taking and sensitivity to peer influence. In one study, children and adolescents were found to be more easily affected by others during a rating task of risk assessments than adults (i.e., age 26-59) (Knoll, Magis-Weinberg, Speekenbrink, & Blakemore, 2015). In the rating task, mid-adolescents (i.e., age 15-18) and young adults (i.e., age 19-25) were more likely to change their

ratings after knowing what others had rated than were adults. Mid-adolescents and young adults relied in particular on the ratings made by adult groups, not by teenage groups. Meanwhile, the ratings made by teenage groups exerted a major influence on the ratings of young adolescents (i.e., age 12-14), indicating that adolescents between the ages of 12 and 14 value peers' opinions noticeably. The risk perception of adolescents and its susceptible nature may be considered a consequence of their enhanced sensitivity to emotions and reduced emotion regulation capacity (Pfeifer et al., 2011).

In the study conducted by Pfeifer et al. (2011), participating adolescents were tested on two occasions: at the age of 10 years (i.e., late childhood, T1) and at the age of 13 years (i.e., early adolescence, T2). In each instance, the adolescent participants underwent fMRI while viewing photographs of emotional expressions (i.e., anger, sadness, happiness, fear, and neutral), and completed two questionnaires that measured the extent of their ability to resist peer influence (using the RPI scale, i.e., Resistance to Peer Influence) and to what extent they had used substances or otherwise reported delinquency (using the IRBD scale, i.e., Indicators of Risk Behaviour and Delinquency). The study aimed to examine the relationship between brain activations that are sensitive to facial emotion recognition and changes in behavioural measures during adolescence. The study showed that activations of ventral striatum (VS) and ventromedial prefrontal cortex (vmPFC) increased from T1 to T2 in the condition of viewing emotional facial expressions, and the increased activity in the VS was associated with viewing photographs of sadness and happiness relative to neutral faces. The increased activation of VS between T1 and T2 was positively correlated with RPI score changes between the two time points, demonstrating that the more adolescents could resist peer influence, the more VS activity was found. The increased VS activity across the two time points was also negatively correlated with changes in IRBD scores, indicating that the greater the reported substance use, the less VS was activated. VS activation, which has been reported to be highly involved in emotion regulation during adolescence (Forbes et al., 2009), is proposed to serve as a form of protection for children or adolescents being influenced by peers (Pfeifer et al., 2011). The evidence highlighted above demonstrates that perceiving facial emotions of sadness and happiness is associated with the ability to resist peer influence during adolescence, which

manifests in neural developmental changes in the brain area involved in emotion regulation. Although other brain areas such as the temporal pole, ventrolateral prefrontal cortex (PFC), and dorsomedial PFC were also found to be sensitive to facial emotions through enhanced activity during adolescence (Moore et al., 2012), there is very little research on the perception of vocal emotional expressions during this transition period.

Vocal emotions like laughter and crying are important in communicating both positive and negative emotions. Indeed, these two vocal emotions are seen at the early stages of life and are thought to be universal across cultures (Sauter et al., 2010). At present, we know relatively little about how typically developing children process emotional vocalizations and how factors such as age and cultural experience play a role in the social learning process.

Nevertheless, we are yet to determine clear evidence of social influences on the perception of laughter and crying. For example, crying is the first emotional vocalization that infants express to interact with their environment. It is also the main way children express negative emotion, although it becomes less frequent over our lifespan. On the other hand, laughter appears to increase in frequency. Babies produce their first laughs at about four months of age and laugh even more frequently as adolescents (Bridges, 1932; Bryant, 1982). It is therefore suggested that experience shapes the way that we express emotional vocalizations, in this case laughing with increased frequency, and crying with reduced frequency.

In life, we probably begin by using vocal emotions involuntarily (e.g., “helpless” laughter or crying), but we can also learn to use vocal emotions communicatively to elicit certain behaviours from our social partners. For example, we laugh to show that we got a joke, or cry to seek attention. We react to the voluntariness of emotions people express, and can correctly categorise involuntary and voluntary laughter (McGettigan et al., 2015). This allows us to ascertain the intention of the vocal expression, which is important knowledge in most everyday social interactions. However, it is clear that the valence of the vocal emotion (e.g., laughing or crying) also affects adults’ perception of voluntariness that neutral stimuli were rated as more authentic than positive ones,

and the positive stimuli were rated as more authentic than negative ones (Fecteau et al., 2005).

In this study, I addressed how the perception of different vocal emotions (laughing and crying) changes over the lifespan. There is pilot data (Scott et al., in prep) suggesting that there are age-related changes in how we react to others' laughter. In particular, children judge the contagion and voluntariness of both voluntary and involuntary laughter differently than adults. However, this dataset does not allow us to judge whether this is true of both positive and negative emotions, and how older adults might differ from younger adults. Understanding how we react to vocal emotions over the lifespan will allow us to understand how age and social experience influence emotional perception. Furthermore, this would be extremely valuable normative information from a clinical perspective, as it can inform studies on those with autism, depression and emotional disorders.

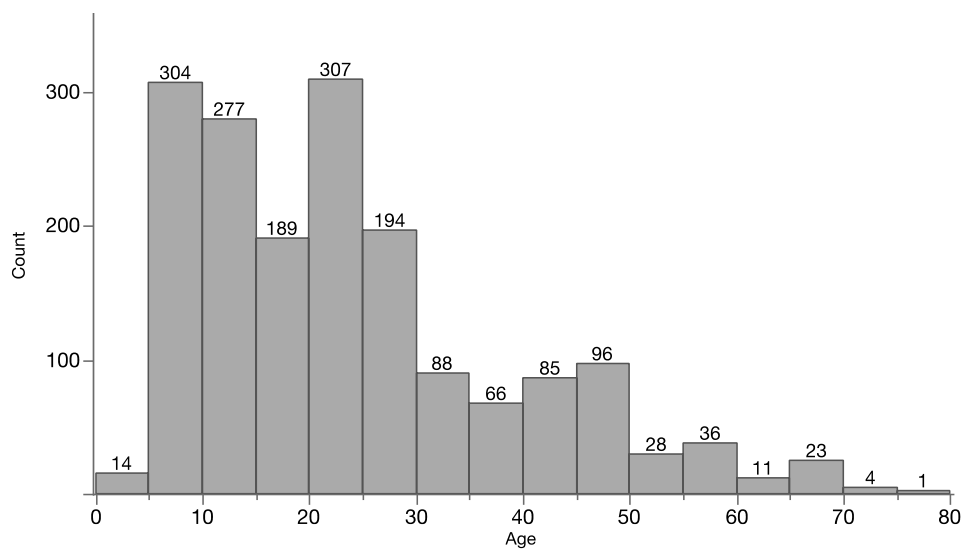
## 4.2 Methods

### 4.2.1 Participants

All participants were recruited at the Science Museum in London as they took part in the Live Science Project – “Who am I?” – during their visit. There were 1,847 healthy participants (age range = 3-76.9 years; mean age = 23; SD = 14.83; 1,067 females) who participated in the experiment and successfully finished the tasks.

Among the 1,847 participants, 119 participants (age range = 3-63 years; mean age = 12.51; SD = 12.91; 55 females) were excluded from further analysis because they correctly answered less than half of the catch trials (i.e., successfully identifying the gender of the speaker in random trials. For more details, see section 4.2.4). Five participants were also excluded because they failed to enter a valid date of birth.

The remaining 1,723 participants (age range = 3-76.9 years; mean age = 23.79; SD = 14.64; 1,010 females) met the criteria of catch trials, resulting in a 62.5% rate of accuracy. The distribution of age shows that participants between six and 30 years old account for 73.7% (n = 1,271) of all participants, and those between 31 and 50 years old account for 19% (n = 335) of all participants. Only 0.06% (n=103) of all participants were over 50 years old (Fig. 4.1). This distribution may reflect the populations who tend to visit the Science Museum as young adults and children represent the majority of visitors and the ageing population represents a smaller portion. Although females account for 58.61% of all participants, female and male participants exhibited a similar distribution of age (Table 4.1).



*Figure 4.1 Age distribution of the participants.*

The figure shows the age distribution of the participants who took part in the experiment and met the criteria of catch trials

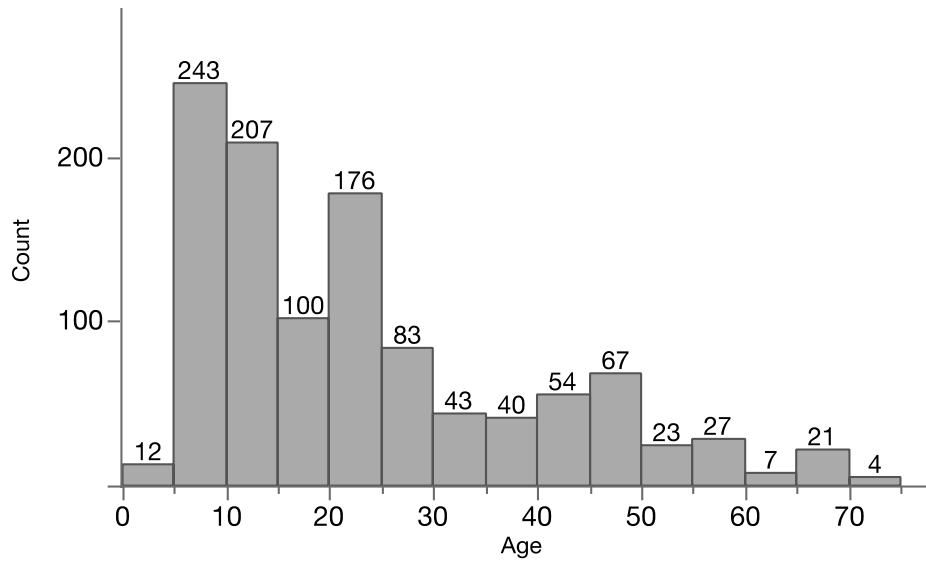
Table 4.1 Age demographics by sex

	Female	Male
Age (years)		
Min	3.67	4.08
Median	21.54	21.50
Mean	23.96	23.55
Max	73.92	76.92
SD	14.73	14.52

Participants were from 72 countries around the world. Participants from the UK accounted for 64.25% (n = 1107) of all participants, followed in abundance by participants from France (n=60), Italy (n=55), Germany (n=52), Spain (n=45), and the United States (n=42) (see Appendix 4.1).

#### 4.2.1.1 The UK profile

Participants from the UK (n=1,107; age range= 3.67-73.92; mean age=23.25; SD = 15.82; 670 females) represent the majority of the sample population. The age distribution of the UK participants (Fig. 4.2) reveals that the majority of the population (66%) was between five and 29 years of age, and the second largest population (19%) was between 30 and 49 years old. The participants between ages 51 and 73 only accounted for 0.07% (n=73; age range= 51-73.91 years; mean age = 60.70 years; SD = 6.29; 48 females) of all participants from the UK. In consideration of this age distribution, the following analysis of the perception of authenticity and contagion by age group only includes participants from age three to 50 (n=1,034; age range= 3.67-50.92 years; mean age = 20.60 years; SD = 12.62, 622 females). The age distribution of the UK participants for females (n =670, age range = 3.67-73.92, mean age = 23.66, SD = 16.07) and males (n= 437, age range = 4.08-71, mean age = 22.62, SD = 15.43) share a similar pattern.



*Figure 4.2 Distribution of age of the UK participants*

#### 4.2.2 Stimuli

The stimuli were selected from the materials (see Chapter 3) and which consisted of 20 stimuli in each condition (i.e., involuntary laughter, voluntary laughter, involuntary crying, and voluntary crying). In involuntary conditions, 10 of the highest authenticity ratings (on a 7-point Likert-Scale) among 20 stimuli in laughter ( $M = 5.97$ ,  $SD = 0.46$ ) or in crying ( $M = 4.59$ ,  $SD = 0.53$ ) were chosen. In voluntary conditions, 10 of the lowest authenticity ratings among 20 stimuli in laughter ( $M = 3.15$ ,  $SD = 0.46$ ) or in crying ( $M = 2.59$ ,  $SD = 0.87$ ) were chosen. The 40 stimuli were presented (average duration = 2.51 seconds;  $SD = 0.38$ ; range = 1.74 – 3.14) with MATLAB (version R2010a, Mathworks, Sherborn, MA, USA) using the psychophysics toolbox (Brainard, 1997; Pelli, 1997) on one of three desktop PCs or two Windows laptops, and were played on headphones (Beyerdynamic DT 770 M) offering approximately 30dB of sound attenuation. Participants were seated approximately 60 cm from the screen and responded by using a mouse.

### 4.2.3 Experimental design

#### *Rating tasks*

All participants rated each stimulus on two different 5-point Likert-scales: authenticity and contagion. For the authenticity ratings, participants rated the extent to which the emotional sound reflected a genuinely-felt emotion by mouse-clicking one of the five icons on the screen to answer the question, ‘How real is the emotion?’ The five icons on the screen were symbols progressing from thumbs down to thumbs up, moving left to right (Fig. 4.3). The icons represented the judgements of very fake, fake, neutral, genuine, and very genuine regarding the emotional sound. The left two thumb icons, which demonstrated ‘fake’ and ‘very fake’ were coloured in red; the middle ‘neutral’ icon was coloured in yellow, and the two icons demonstrating ‘genuine’ and ‘very genuine’ on the right were coloured in green. For the contagion ratings, participants rated the extent to which the emotional sound was contagious by mouse-clicking one of the five icons on the screen to answer the question, ‘How much do you want to join in?’ To provide a clear visual demonstration of laughter or crying, laughing faces or crying faces respectively displayed on the screen for laughter or crying trials. In the laughter trials, the icons on the screen progressed from left to right from an animated neutral face to a smiling face through alternations in the shape of the mouth, representing different levels of willingness that the participants felt to laugh along with the sound (Fig. 4.4). In the crying trials, the icons were replaced by faces progressing from neutral to crying, representing different levels of willingness that the participants felt to cry along with the sounds (Fig. 4.4).

#### *Experimental design*

There were four blocks in the experiment, and each block targeted either authenticity ratings or contagion ratings. The order of these two rating scales was counterbalanced, and each participant was randomly assigned to one of the orders of rating scales. There were 20 stimuli per block, resulting in 80 trials in the whole experiment. Each block consisted of two mini-blocks of 10 stimuli each, pertaining to the two expressions (i.e., one mini-block consisted of 10 laughter or 10 crying sounds). The 10 stimuli in each expression were randomly



selected from 20 laughter or crying stimuli, including involuntary and voluntary vocalisations. The order of mini-blocks was counterbalanced for each rating scale (see Fig. 4.5 for an example of experimental structure).

At the beginning of each block, a screen appeared to instruct which type of ratings would follow (i.e., authenticity ratings or contagion ratings). The first trial began after participants clicked a start button. There were eight catch trials in the experiment to ensure that instruction was comprehended correctly and participants paid attention to the stimuli. One catch trial randomly appeared in the middle of each mini-block (i.e., after the first four trials and before the last trial), resulting in two catch trials per block. The catch trials, which appeared directly after participants responded to a rating trial, required the participants to recall whether the last emotional sound they heard was produced by a female or male speaker. The participants responded by clicking one of the figures on the screen representing 'female' or 'male' voices. After the participants had rated an emotional sound or finished a catch trial, the next trial immediately started.

At the beginning of the experiment, a video with auditory instructions explained the trial procedure including the two rating tasks and catch trials. At the end of the experiment, a screen displayed individualised feedback to each participant to report how they performed on differentiating involuntary vocalisations from voluntary vocalisations, and which expressions they found more contagious. Each experiment lasted approximately 15 minutes.

### *Procedure*

Lab members approached visitors of the Life Science Project at the Science Museum in London and introduced the purpose and procedure of the experiment to them. The participants were then given a consent form describing the participants' rights while partaking in the experiment and an information sheet of experimental details. Parents accompanied all minors under the age of 18, and both parents and minor participants were informed that the experiment involved crying sounds that while commonly heard in everyday life, could influence the participant. Before entering the experimental program, all

participants signed the consent forms, and both children and their parents signed a consent form in the case of minors.

After signing the consent forms, all participants were introduced to the experimental program and guided to fill in their demographic information. Before the rating task started, each participant confirmed that he or she understood the task and had the opportunity to ask any questions. After they finished the experiment, participants received a debrief card were once again allowed to ask questions.



Figure 4.3 Authenticity rating scale



Figure 4.4 Contagion rating scales for laughter (top) and crying (bottom)

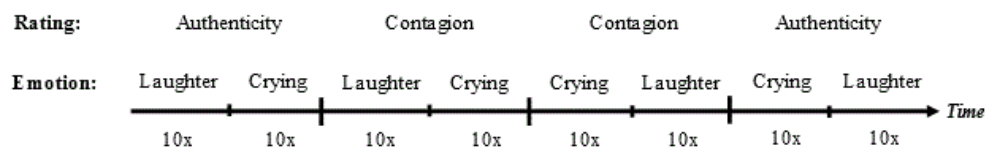


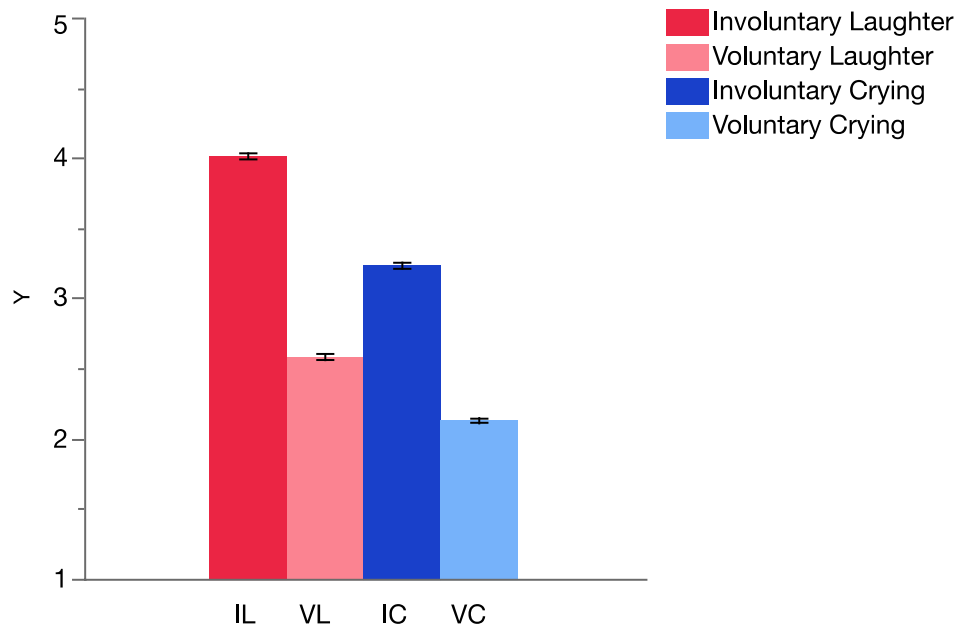
Figure 4.5 Counterbalancing in the experimental design

### 4.3 Results

Although the 1,723 participants were from 72 different countries, the numbers of participants were not equally spread across these countries. Participants from countries other than the UK (i.e., the other 71 countries) only accounted for 36% of participants ( $n = 616$ ). To reduce the possibility that a large variation could arise from the wide-spread, unequally distributed populations from the 72 countries, only participants from the UK ( $n = 1107$ ) were included in the following analyses.

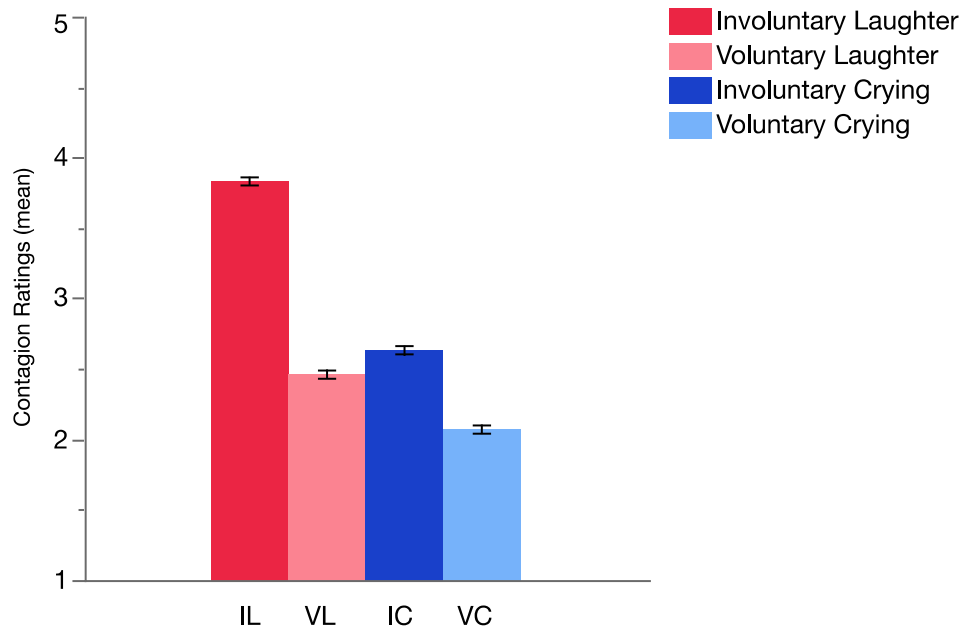
#### 4.3.1 Rating results

A 2 x 2 ANOVA was conducted for each authenticity and contagion scale, including expression (laughter/crying) and involuntariness (involuntary/voluntary) as repeated-measures factors. On the authenticity scale, involuntary laughter ( $M = 4.01$ ;  $SD = 0.63$ ) and involuntary crying ( $M = 3.25$ ;  $SD = 0.69$ ) were rated higher (i.e., more authentic) than voluntary laughter ( $M = 2.57$ ;  $SD = 0.70$ ) and voluntary crying ( $M = 2.11$ ;  $SD = 0.61$ ; main effect of authenticity,  $F[1,1106] = 3779.36$ ,  $MSE = .490$ ,  $p < .001$ ,  $\eta_p^2 = .774$ ). The main effect of expression was also significant, indicating that laughter was generally rated as more authentic than crying ( $F[1, 1106] = 1126.97$ ,  $MSE = .365$ ,  $p < .001$ ,  $\eta_p^2 = .505$ ). The effect of interaction was also significant ( $F[1, 1106] = 176.84$ ,  $MSE = .151$ ,  $p < .001$ ,  $\eta_p^2 = .138$ ) according to paired sample t-tests that showed significant differences both in the perceived authenticity of laughter (involuntary:  $M = 4.02$ ,  $SD = 0.63$ ; voluntary:  $M = 2.57$ ,  $SD = 0.70$ ;  $t(1106) = 58.00$ ,  $p < .001$ , Cohen's  $d = 2.18$ ), and of crying (involuntary:  $M = 3.25$ ,  $SD = 0.69$ ; voluntary:  $M = 2.11$ ,  $SD = 0.61$ ;  $t(1106) = 49.26$ ,  $p < .001$ , Cohen's  $d = 1.75$ ). The results indicate that involuntary vocalizations are perceived as more genuine than voluntary ones, and that laughter is generally rated more authentic than crying. Moreover, the perceived difference in authenticity between involuntary and voluntary laughter was greater than that between involuntary and voluntary crying (Fig. 4.6).



*Figure 4.6 Results of authenticity ratings from UK participants*

On the contagion scale, involuntary laughter ( $M = 3.84$ ;  $SD = 0.78$ ) and involuntary crying ( $M = 2.63$ ;  $SD = 0.94$ ) were rated as more contagious (i.e., more contagious) than voluntary laughter ( $M = 2.45$ ;  $SD = 0.84$ ) and voluntary crying ( $M = 2.06$ ;  $SD = 0.87$ ; main effect of involuntariness,  $F[1,1106] = 2272.23$ ,  $MSE = .465$ ,  $p < .001$ ,  $\eta_p^2 = .673$ ). The main effect of expression was significant, indicating that laughter was generally rated as more contagious than crying ( $F[1, 1106] = 970.10$ ,  $MSE = .729$ ,  $p < .001$ ,  $\eta_p^2 = .467$ ). The effect of interaction was also significant ( $F[1, 1106] = 896.24$ ,  $MSE = .203$ ,  $p < .001$ ,  $\eta_p^2 = .448$ ) according to paired sample t-tests that showed significant differences both in the perceived contagiousness of laughter (involuntary:  $M = 3.84$ ,  $SD = 0.78$ ; voluntary:  $M = 2.45$ ,  $SD = 0.84$ ;  $t(1106) = 52.18$ ,  $p < .001$ , Cohen's  $d = 1.71$ ) and of crying (involuntary:  $M = 2.63$ ,  $SD = 0.94$ ; voluntary:  $M = 2.06$ ,  $SD = 0.87$ ;  $t(1106) = 25.52$ ,  $p < .001$ , Cohen's  $d = 0.63$ ). The results support the conclusion that involuntary vocalizations are perceived as more contagious than voluntary ones, and that laughter is generally rated more contagious than crying (Fig. 4.7). However, it is worth mentioning that the difference between the perceived contagiousness of involuntary and voluntary crying was much smaller than the difference between involuntary and voluntary laughter, which results in a lower Cohen's  $d$  value.



*Figure 4.7 Results of contagion ratings from UK participants*

The rating results were divided by age group to investigate how the perception of authenticity or contagion changes according to age. The following analyses included the participants from ages three to 50 ( $n=1034$ , age range = 3.67-50.92 years, mean age = 20.60 years, SD = 12.62, 622 females). The participants were divided into four age groups: 368 children (age range: 3.67-11.91 years, mean age = 8.66 years, SD = 1.98, 218 females), 148 adolescents (age range: 12-18.92 years, mean age = 14.68 years, SD = 2.22, 90 females), 305 young adults (age range: 19- 29.91 years, mean age = 23.37 years, SD = 2.88, 184 females), and 213 adults (age range: 30-50.92 years, mean age = 41.39 years, SD = 6.03, 129 females).

#### 4.3.1.1 Interactions between involuntariness, emotions, and age group on each rating scale

A three-way ANOVA was first used to test whether there was any interaction between the perception of authenticity of emotional vocalizations and age group. This resulted in a three-factorial mixed design with the two within-subject factors -expressions (laughter and crying) and involuntariness (involuntary and voluntary) - and the between-subjects factor group (age). Greenhouse-Geisser corrections were used and significance levels for pairwise comparisons were Tukey-HSD corrected and reported two-tailed.

##### *The authenticity scale*

There was a main effect of expression ( $F(1,1030) = 949.80$ ,  $MSE = .357$ ,  $p < .001$ ,  $\eta_p^2 = .480$ ), revealing that laughter ( $M = 3.30$ ,  $SD = 0.51$ ) was rated more authentic than crying ( $M = 2.68$ ,  $SD = 0.53$ ). No significant difference was found between expressions and age groups ( $F(3,1030) = .945$ ,  $MSE = .357$ ,  $p = .418$ ,  $\eta_p^2 = .003$ ), indicating that there was no difference in the perception of authenticity between laughter and crying across age groups (Fig. 4.8).

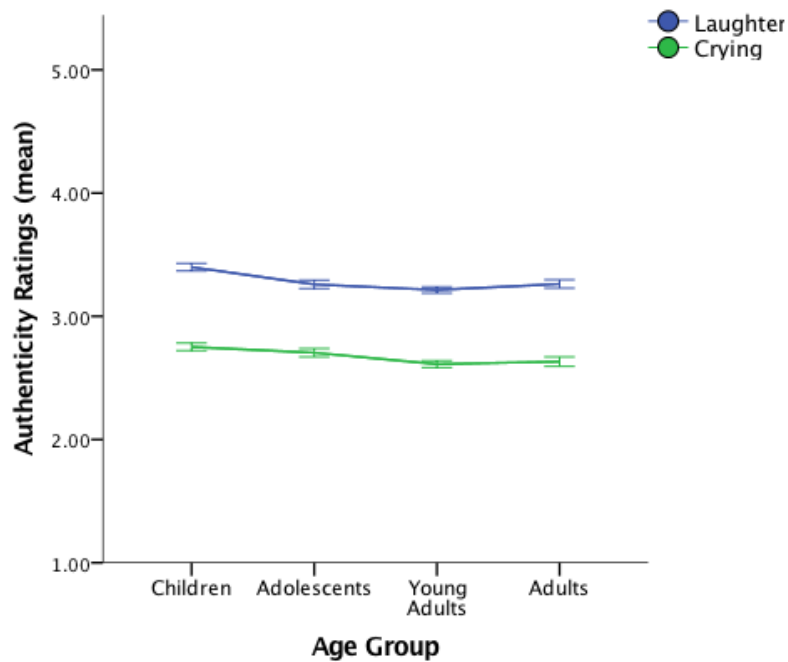


Figure 4.8 Authenticity results of expressions across age groups.

There was a main effect of involuntariness ( $F(1,1030) = 4857.16$ ,  $MSE = .336$ ,  $p < .001$ ,  $\eta_p^2 = .825$ ), indicating that involuntary vocalisations ( $M = 3.62$ ,  $SD = 0.55$ ) were rated more authentic than voluntary vocalisations ( $M = 2.35$ ,  $SD = 0.56$ ). There was also a significant interaction between involuntariness and age groups ( $F(3,1030) = 164.387$ ,  $MSE = .336$ ,  $p < .001$ ,  $\eta_p^2 = .324$ ), indicating that the difference in the perception of authenticity between involuntary and voluntary vocalisations changed across age groups.

A one-way ANOVA was then conducted for each condition of involuntariness across age groups. There was a main effect of age group on the authenticity perception of involuntary vocalisations ( $F(3,1030) = 22.11$ ,  $p < .001$ ). Children ( $M = 3.45$ ,  $SD = 0.55$ ) rated involuntary vocalisations as less authentic than did all other age groups, including adolescents ( $M = 3.65$ ,  $SD = 0.49$ ,  $p = .001$ ); young adults ( $M = 3.71$ ,  $SD = 0.51$ ,  $p < .001$ ); and adults ( $M = 3.78$ ,  $SD = 0.57$ ,  $p < .001$ ). No other pairwise comparison was significant, including adolescents compared with young adults ( $p = .656$ ); adolescents compared with adults ( $p = .112$ ); and young adults compared with adults ( $p = .504$ ). There was also a main effect of age group on the authenticity perception of voluntary vocalisations ( $F(3,1030) = 99.66$ ,  $p < .001$ ). Children ( $M = 2.70$ ,  $SD = 0.55$ ) rated voluntary vocalisations as more authentic than did all other age groups, including adolescents ( $M = 2.31$ ,  $SD = 0.42$ ,  $p < .001$ ); young adults ( $M = 2.12$ ,  $SD = 0.44$ ,  $p < .001$ ); and adults ( $M = 2.12$ ,  $SD = 0.51$ ,  $p < .001$ ). Adolescents rated voluntary vocalisations as more authentic than did both young adults ( $p < .001$ ) and adults ( $p = .001$ ). However, young adults and adults rated voluntary vocalisations with no difference ( $p = 1.00$ ) (Fig. 4.9).

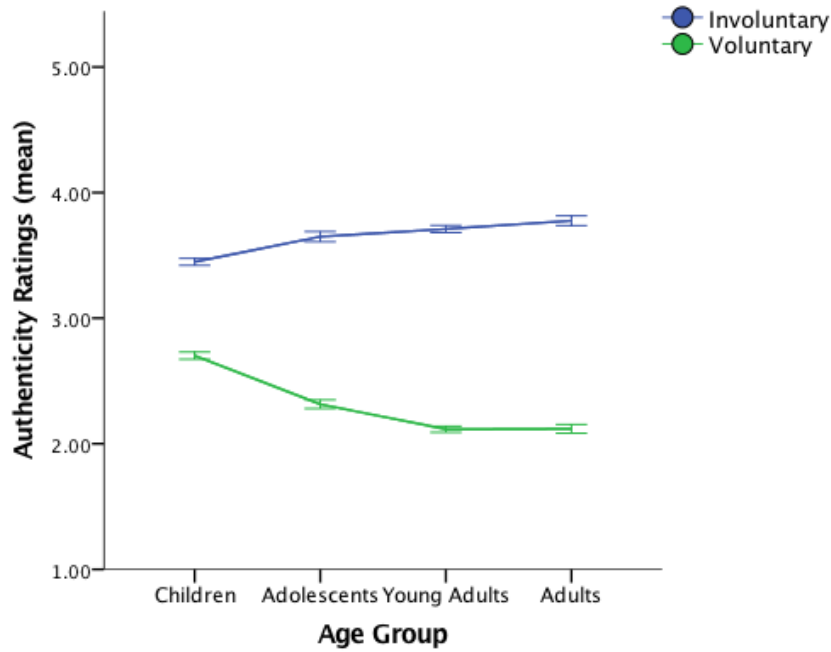


Figure 4.9 Authenticity results of involuntariness across age groups.

There was a significant interaction between involuntariness and expressions ( $F(1,1030) = 161.24$ ,  $MSE = .152$ ,  $p < .001$ ,  $\eta_p^2 = .135$ ). Post-hoc paired-sample t-tests were conducted to compare the authenticity ratings for the involuntary vocalisations to the voluntary vocalisations in each expression. There were significant differences in the authenticity ratings for involuntariness in both laughter and crying, signalling that involuntary laughter ( $M = 4.01$ ,  $SD = 0.63$ ) was rated more authentic than voluntary laughter ( $M = 2.58$ ,  $SD = 0.70$ ),  $t(1033) = 54.95$ ,  $p < .001$ , and that involuntary crying ( $M = 3.23$ ,  $SD = 0.69$ ) was rated more authentic than voluntary crying ( $M = 2.13$ ,  $SD = 0.62$ ),  $t(1033) = 46.22$ ,  $p < .001$ ) (Fig. 4.10). There was no significant three-way interaction between involuntariness, expressions, and age groups ( $F(3,1030) = 1.209$ ,  $MSE = .152$ ,  $p = .305$ ,  $\eta_p^2 = .004$ ).



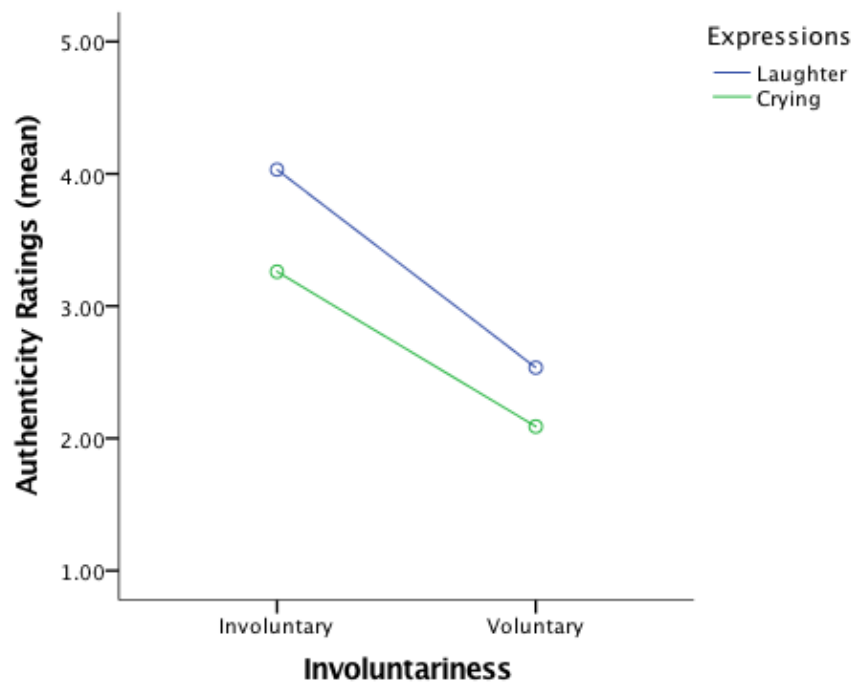


Figure 4.10 Authenticity ratings of involuntariness and expressions.

*The contagion scale*

There was a main effect of expressions ( $F(1,1030) = 817.553$ ,  $MSE = .723$ ,  $p < .001$ ,  $\eta_p^2 = .443$ ), illustrating that laughter ( $M = 3.15$ ,  $SD = 0.68$ ) was rated as more contagious than crying ( $M = 2.35$ ,  $SD = 0.83$ ). There was also a significant interaction between expressions and age group ( $F(3,1030) = 2.640$ ,  $MSE = .723$ ,  $p = .048$ ,  $\eta_p^2 = .008$ ), indicating that the difference between contagion ratings of laughter and crying significantly differed between age groups (Fig. 4.11).

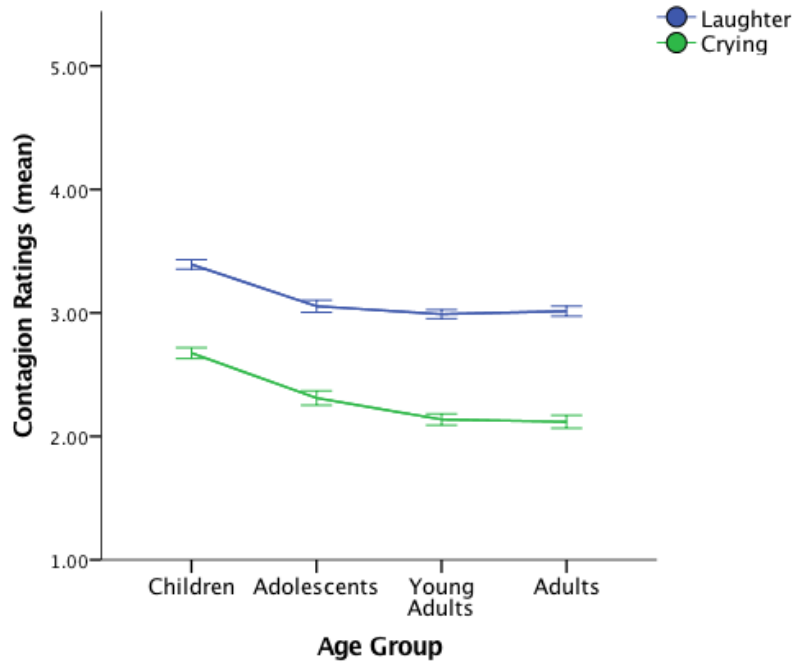
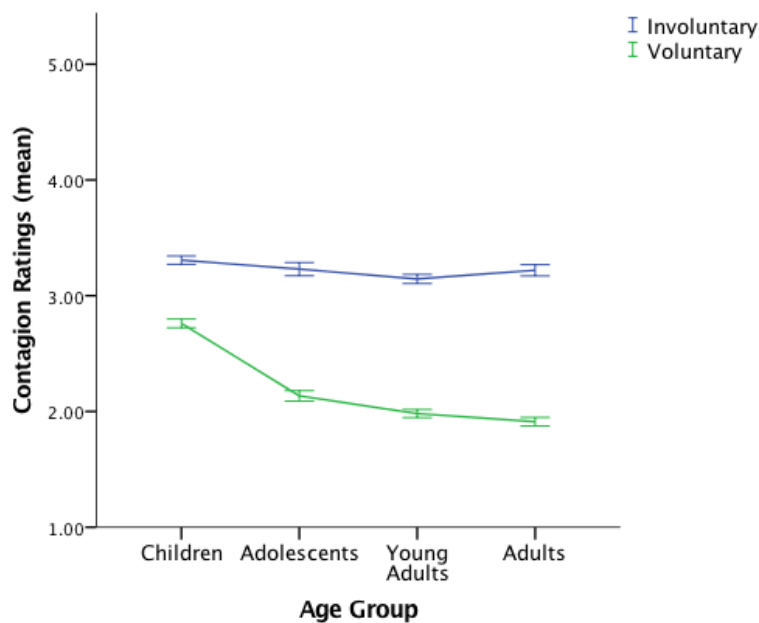


Figure 4.11 Contagion ratings of expressions across age groups.

Two one-way ANOVAs were separately conducted for laughter and crying to test whether the contagion ratings changed significantly across age groups for each expression. There was a significant main effect of age group on the contagion ratings of laughter ( $F(3,1030) = 26.68, p < .001$ ). Children rated laughter as more contagious than did all other groups, including adolescents ( $M = 3.05, SD = 0.60, p < .001$ ); young adults ( $M = 2.99, SD = 0.64, p < .001$ ); and adults ( $M = 3.01, SD = 0.60, p < .001$ ). No other pairwise comparison was significant, including adolescents compared with young adults ( $p = .766$ ); adolescents compared with adults ( $p = .94$ ); and young adults compared with adults ( $p = .98$ ). There was also a significant main effect of age group on the contagious ratings of crying ( $F(3,1030) = 34.084, p < .001$ ). Children ( $M = 2.67, SD = 0.84$ ) rated crying as more contagious than did all other groups, including adolescents ( $M = 2.31, SD = 0.71, p < .001$ ); young adults ( $M = 2.14, SD = 0.79, p < .001$ ); and adults ( $M = 2.12, SD = 0.76, p < .001$ ). No other pairwise comparison was significant, including adolescents compared with young adults ( $p = .13$ ); adolescents compared with adults ( $p = .11$ ); and young adults compared with adults ( $p = .99$ ).

There was a main effect of involuntariness ( $F(1,1030) = 2687.334$ ,  $MSE = .361$ ,  $p < .001$ ,  $\eta_p^2 = .723$ ), demonstrating that involuntary vocalisations ( $M = 3.23$ ,  $SD = 0.70$ ) were rated more contagious than voluntary ones ( $M = 2.27$ ,  $SD = 0.73$ ). There was also a significant interaction between involuntariness and age group ( $F(3,1030) = 96.023$ ,  $MSE = .361$ ,  $p < .001$ ,  $\eta_p^2 = .219$ ), indicating that the difference between involuntary and voluntary vocalisations changed across age groups (Fig. 4.12).



*Figure 4.12 Contagion results of involuntariness across age groups.*

A follow-up one-way ANOVA was conducted for each condition of involuntariness. This test revealed a main effect of age group on the contagion ratings of involuntary vocalisations ( $F(3,1030) = 3.059$ ,  $p = .027$ ). Children ( $M = 3.31$ ,  $SD = 0.69$ ) rated involuntary vocalisations as more contagious than young adults ( $M = 3.14$ ,  $SD = 0.69$ ,  $p = .014$ ). No other pairwise comparison was significant, including children compared with adolescents ( $M = 3.23$ ,  $SD = 0.69$ ,  $p = .661$ ); children compared with adults ( $M = 3.22$ ,  $SD = 0.71$ ,  $p = .463$ ); adolescents compared with young adults ( $p = .614$ ); adolescents compared with adults ( $p = 1.00$ ); and young adults compared with adults ( $p = .620$ ). The test also

found a main effect of age group on the contagion ratings of voluntary vocalisations ( $F(3,1030) = 119.261, p < .001$ ). Children ( $M = 2.76, SD = 0.72$ ) rated voluntary vocalisations as more contagious than did all other groups, including adolescents ( $M = 2.13, SD = 0.55, p < .001$ ); young adults ( $M = 1.98, SD = 0.62, p < .001$ ); and adults ( $M = 1.91, SD = 0.53, p < .001$ ). Furthermore, adolescents rated voluntary vocalisations as more contagious than did adults ( $p = .006$ ). No other pairwise comparison was significant, including adolescents compared with young adults ( $p = .077$ ) and young adults compared with adults ( $p = .603$ ).

There was a significant interaction between expressions and involuntariness on the contagion ratings ( $F(1,1030) = 842.312, MSE = .194, p < .001, \eta_p^2 = .450$ ). Post-hoc paired-sample t-tests were utilized to compare the contagion ratings of the involuntary vocalisations to voluntary vocalisations in each expression. There were significant differences in the contagion ratings of involuntariness in both laughter and crying, indicating that involuntary laughter ( $M = 3.83, SD = 0.78$ ) was rated more contagious than voluntary laughter ( $M = 2.46, SD = 0.84, t(1033) = 49.89, p < .001$ ), and that involuntary crying ( $M = 2.63, SD = 0.94$ ) was rated more contagious than voluntary crying ( $M = 2.07, SD = 0.87, t(1033) = 24.33, p < .001$ ) (Fig. 4.13).

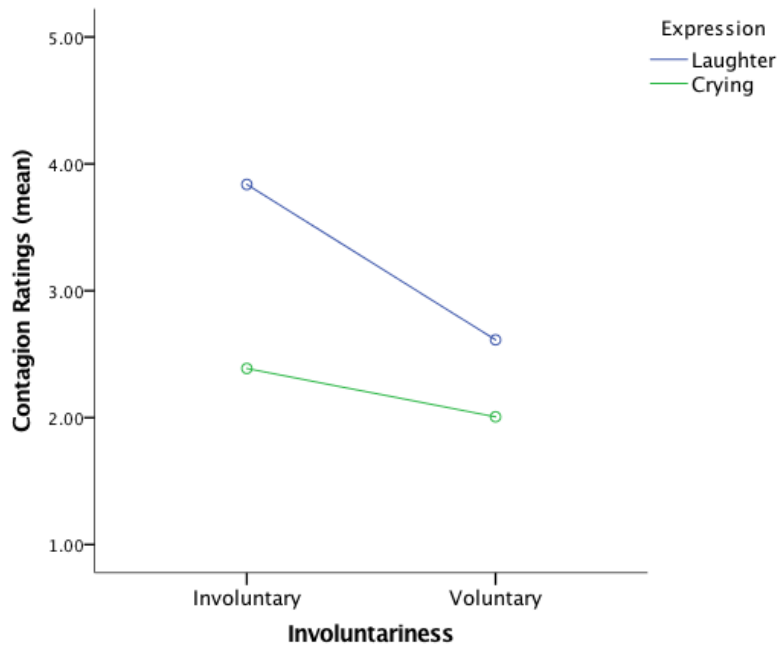


Figure 4.13 Contagion results between involuntariness and expressions

Finally, there was a significant three-way interaction between expressions, involuntariness, and age group on the contagion ratings ( $F(3,1030) = 14.274$ ,  $MSE = .194$ ,  $p < .001$ ,  $\eta_p^2 = .04$ ). The follow-up two-way ANOVAs were separately conducted under each expression to test whether the perceived differences in contagiousness between involuntary and voluntary vocalisations differs across age groups in laughter or in crying. A 2 x 4 ANOVA was conducted for each expression, using involuntariness and age group as within- and between-subjects repeated-measures factors.

For the laughter expression (Fig. 4.14), there was a main effect of involuntariness ( $F(1,1030) = 3120.668$ ,  $MSE = .309$ ,  $p < .001$ ,  $\eta_p^2 = .752$ ), indicating that involuntary laughter ( $M = 3.83$ ,  $SD = 0.78$ ) was rated more contagious than voluntary laughter ( $M = 2.46$ ,  $SD = 0.84$ ). There was also a significant interaction between involuntariness and age group ( $F(3,1030) = 91.570$ ,  $MSE = .309$ ,  $p < .001$ ,  $\eta_p^2 = .211$ ), showing that the difference between involuntary laughter and voluntary laughter in contagion ratings varied across age groups. Therefore, the two following one-way ANOVAs were individually

conducted for involuntary laughter and for voluntary laughter to test whether the contagion ratings of each condition differed across age groups.

The results of the one-way ANOVA performed on the involuntary laughter expression revealed that there was no main effect of age group on the perception of the contagiousness of involuntary laughter ( $F(3,1030) = .792, p = .498$ ; children:  $M = 3.81, SD = 0.82$ ; adolescents:  $M = 3.82, SD = 0.78$ ; young adults:  $M = 3.81, SD = 0.77$ ; adults:  $M = 3.91, SD = 0.74$ ). This finding demonstrates there was no age group difference in perceiving the contagious level of involuntary laughter. However, there was a main effect of age group on the perception of contagiousness of voluntary laughter ( $F(3,1030) = 89.99, p < .001$ ). Children rated voluntary laughter as more contagious ( $M = 2.98, SD = 0.86$ ) than all other age groups, including adolescents ( $M = 2.29, SD = 0.65, p < .001$ ); young adults ( $M = 2.16, SD = 0.72, p < .001$ ); and adults ( $M = 2.12, SD = 0.65, p < .001$ ). No other pairwise comparison was significant, including adolescents compared with young adults ( $p = .36$ ); adolescents compared with adults ( $p = .16$ ); and young adults compared with adults ( $p = .92$ ).

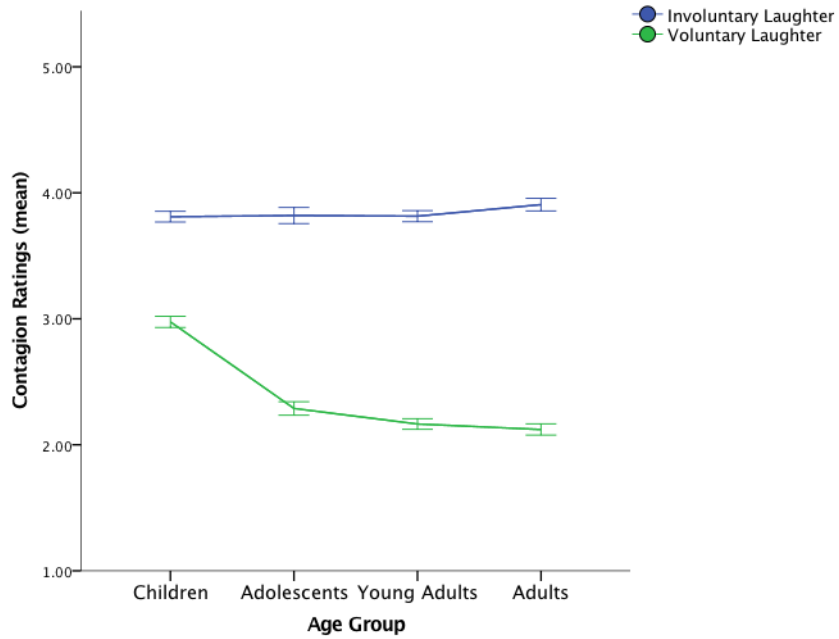


Figure 4.14 Contagion results of laughter across age group.

The additional 2x4 ANOVA with involuntariness and age group as repeated measures was conducted for the crying vocalisations. This test found a main effect of involuntariness on the contagion ratings of crying vocalisations ( $F(1,1030) = 687.18$ ,  $MSE = .246$ ,  $p < .001$ ,  $\eta_p^2 = .40$ ), indicating that involuntary crying ( $M = 2.63$ ,  $SD = 0.94$ ) was rated more contagious than voluntary crying ( $M = 2.07$ ,  $SD = 0.87$ ). There was also a significant interaction between involuntariness and age group ( $F(3,1030) = 37.162$ ,  $MSE = .246$ ,  $p < .001$ ,  $\eta_p^2 = .098$ ), showing that the difference in contagion ratings between involuntary and voluntary crying varied across age group (Fig. 4.15). Following this test, two one-way ANOVAs were conducted to examine each condition of crying.

There was a main effect of age group on the perception of contagion for involuntary crying ( $F(3,1030) = 7.809$ ,  $p < .001$ ). Children ( $M = 2.80$ ,  $SD = 0.91$ ) rated involuntary crying with no significant difference when compared with adolescents ( $M = 2.64$ ,  $SD = 0.87$ ,  $p = .27$ ), but rated it as more contagious than did both young adults ( $M = 2.48$ ,  $SD = 0.94$ ,  $p < .001$ ) and adults ( $M = 2.53$ ,  $SD = 1.00$ ,  $p = .004$ ). No other pairwise comparison was significant, including adolescents compared with young adults ( $p = .29$ ); adolescents compared with adults ( $p = .71$ ); and young adults compared with adults ( $p = .90$ ).

For voluntary crying, there was also a main effect of age group on the contagion ratings ( $F(3,1030) = 71.523, p < .001$ ). Children rated voluntary crying as more contagious than did every other age group ( $M = 2.55, SD = 0.91$ ), including adolescents ( $M = 1.98, SD = 0.68, p < .001$ ); young adults ( $M = 1.80, SD = 0.78, p < .001$ ); and adults ( $M = 1.70, SD = 0.66, p < .001$ ). Adolescents rated voluntary crying with no significant difference when compared with young adults ( $p = .10$ ), but rated it as more contagious than did adults ( $p = .006$ ). No significant difference was found between the ratings of young adults and adults ( $p = .52$ ).

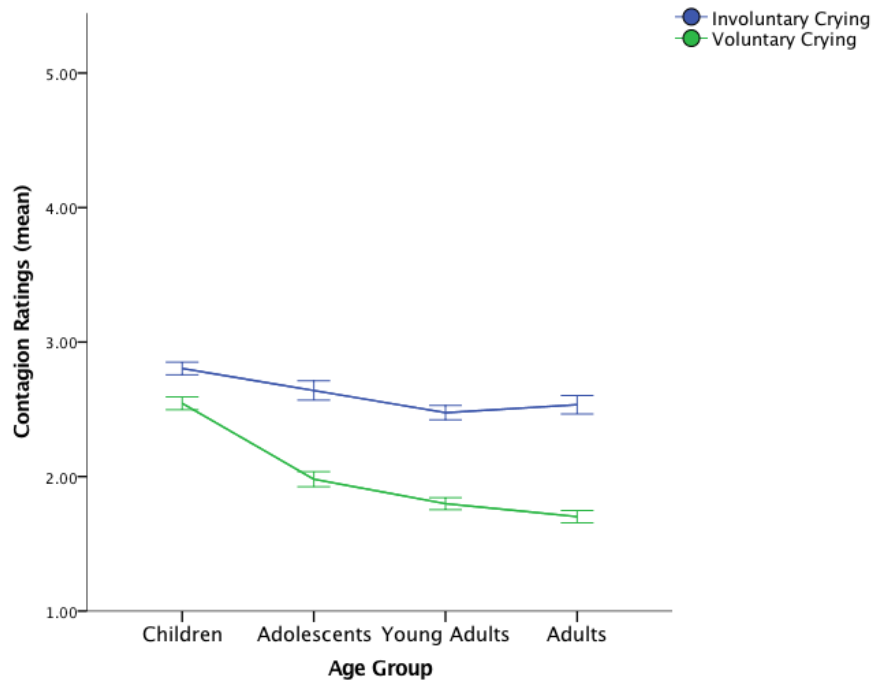


Figure 4.15 Contagion results of crying by age group.



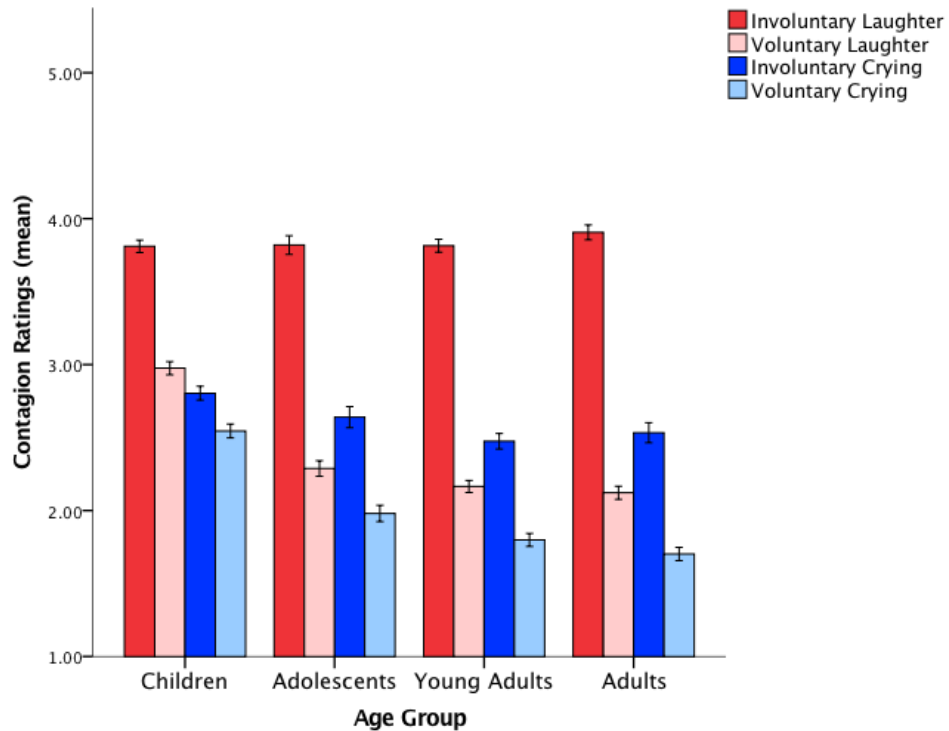
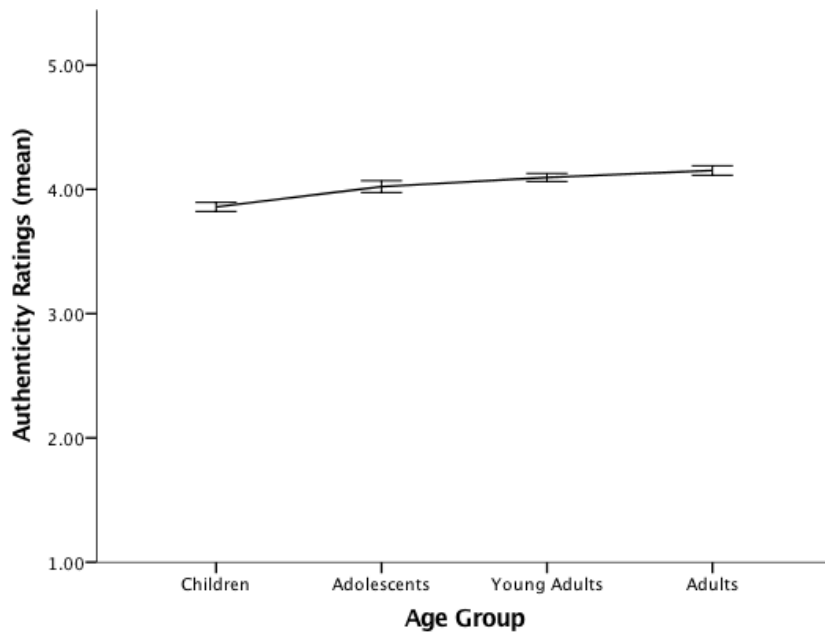


Figure 4.16 Contagion ratings of four conditions across age groups

#### One-way ANOVA on authenticity ratings

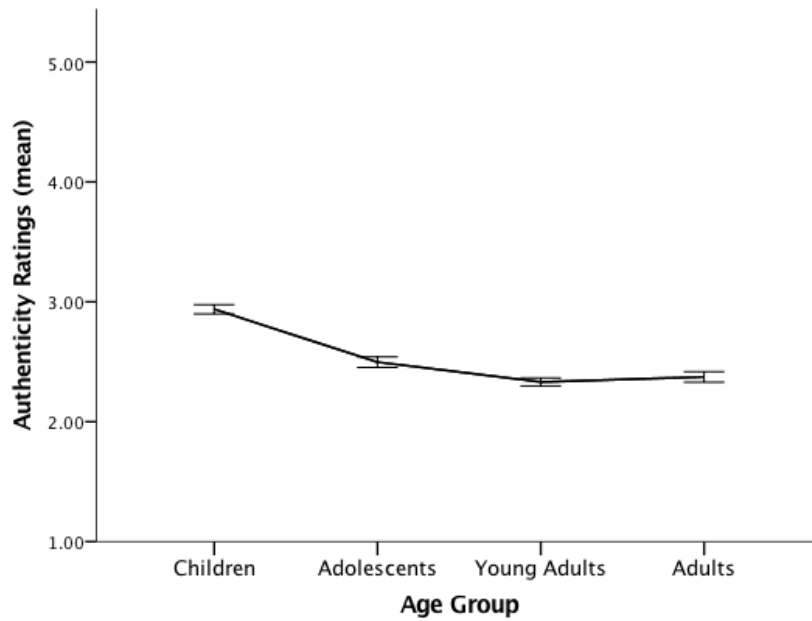
To better understand how the perception of authenticity in each condition varied from childhood to adulthood, a one-way ANOVA was utilized for condition to test whether the perception of authenticity differed across age groups. Post hoc pairwise comparisons (Tukey's HSD-adjusted alpha levels) were used to compare the authenticity ratings between age groups when there was a significant interaction effect.

There was a main effect of age group on the authenticity perception of involuntary laughter ( $F(3,1030) = 13.097, p < .001$ ). Children rated involuntary laughter as less authentic ( $M = 3.86, SD = 0.70$ ) than did every other age group, including adolescents ( $M = 4.02, SD = 0.57, p = .034$ ); young adults ( $M = 4.10, SD = 0.66, p < .001$ ); and adults ( $M = 4.15, SD = 0.56, p < .001$ ). No other pairwise comparison was significant, including adolescents compared with young adults ( $p = 1.00$ ); adolescents compared with adults ( $p = .29$ ); and young adults compared with adults ( $p = 1.00$ ) (Fig. 4.17).



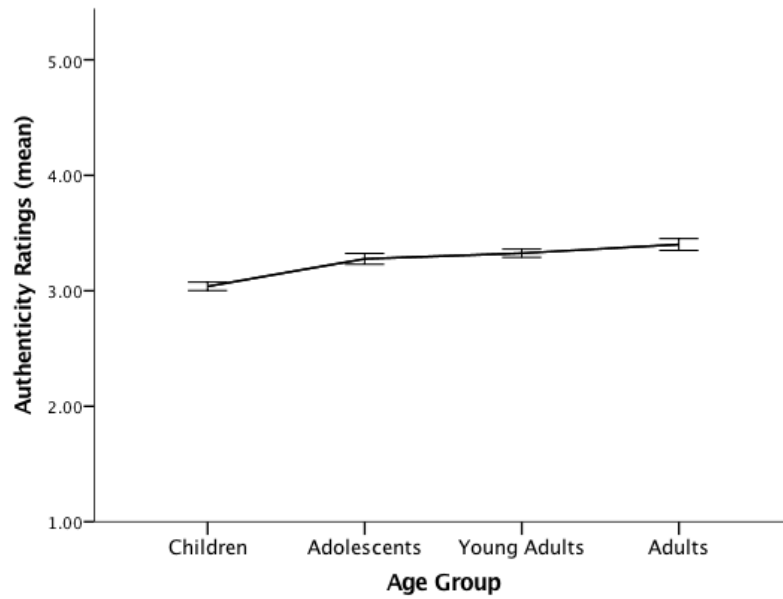
*Figure 4.17 Authenticity results of involuntary laughter across age groups.*

There was also a main effect of age group on the perception of authenticity of voluntary laughter ( $F(3,1030) = 61.442, p < .001$ ). Children rated the voluntary laughter as more authentic ( $M = 2.94, SD = 0.38$ ) than did every other age group, including adolescents ( $M = 2.50, SD = 0.53, p < .001$ ); young adults ( $M = 2.33, SD = 0.58, p < .001$ ); and adults ( $M = 2.37, SD = 0.64, p < .001$ ). No other pairwise comparison was significant among adolescents compared with adults ( $p = .28$ ) and young adults compared with adults ( $p = .89$ ). Adolescents did rate the voluntary laughter more authentic than did young adults, but this result was only marginally significant ( $p = .052$ ) (Fig. 4.18).



*Figure 4.18 Authenticity results of voluntary laughter across age group.*

There was a main effect of age group on the perception of authenticity of involuntary crying ( $F(3,1030) = 16.692, p < .001$ ). Children rated the involuntary crying as less authentic ( $M = 3.04, SD = 0.70$ ) than did every other age group, including adolescents ( $M = 3.27, SD = 0.57, p = .002$ ); young adults ( $M = 3.33, SD = 0.64, p < .001$ ); and adults ( $M = 3.40, SD = 0.74, p < .001$ ). No other pairwise comparison was significant, including adolescents compared with young adults ( $p = .89$ ); adolescents compared with adults ( $p = .31$ ); and young adults compared with adults ( $p = .59$ ) (Fig. 4.19).



*Figure 4.19 Authenticity results for involuntary crying by age group.*

There was a main effect of age group on the perception of authenticity of voluntary crying ( $F(3,1030) = 76.71, p < .001$ ). Children rated the voluntary crying as more authentic ( $M = 2.46, SD = 0.65$ ) than did every other age group, including adolescents ( $M = 2.13, SD = 0.49, p < .001$ ); young adults ( $M = 1.90, SD = 0.48, p < .001$ ); and adults ( $M = 1.86, SD = 0.55, p < .001$ ). Adolescents rated voluntary crying as more authentic than did young adults ( $p < .001$ ) and adults ( $p < .001$ ). No significant difference was found between young adults and adults ( $p = .89$ ) (Fig. 4.17).

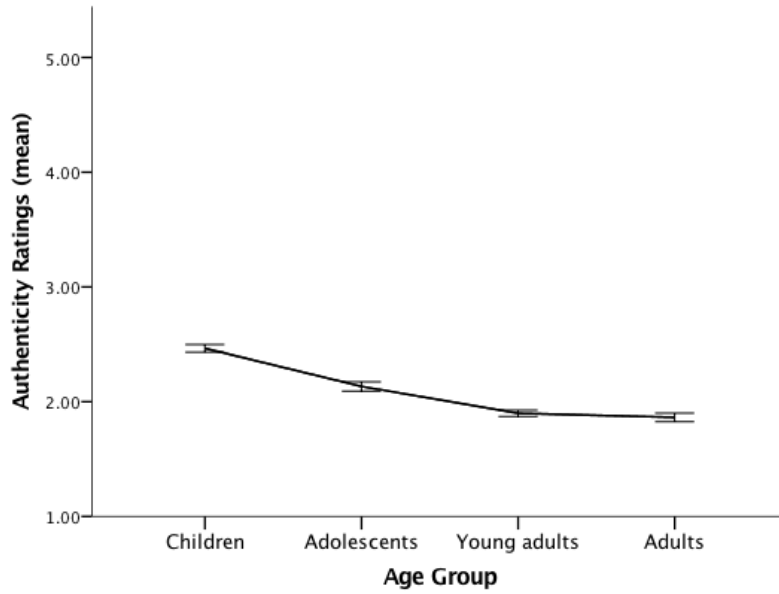


Figure 4.20 Authenticity results for voluntary crying by age group.

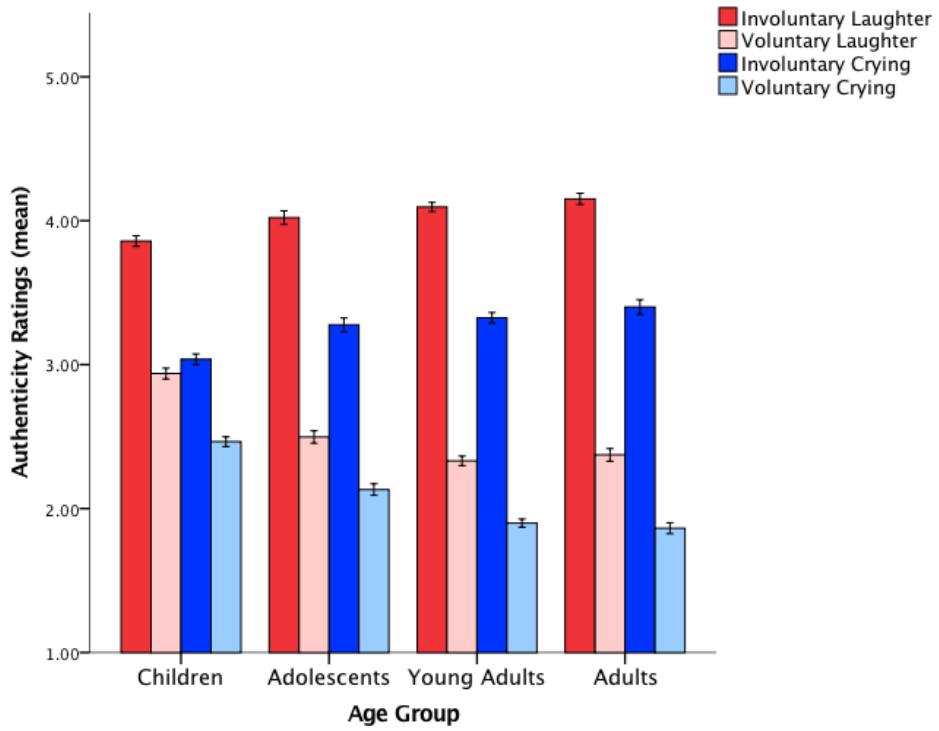


Figure 4.21 Authenticity ratings of four conditions across age groups

### 4.3.2 Regression

To understand the relationship between age and perceptions of authenticity or contagiousness for emotional vocalisations, a regression analysis was used for each condition on two rating scales. Because developmental trajectories are better described by reciprocally transforming participants' age as predictors than by fitting the trajectories with straight lines (Leech, Aydelott, Symons, Carnevale, & Dick, 2007), non-linear regression models were applied to fit the shape of rating results across age groups.

#### *Authenticity scale*

A non-linear regression analysis was used to test whether age significantly predicted participants' authenticity ratings of involuntary laughter, voluntary laughter, involuntary crying, and voluntary crying. For involuntary laughter, the results of the regression indicated that the predictor (age) explained 3.72% of the variance in ratings ( $F(1,1032) = 39.88, p < .001, R^2 = .037$ , spearman's rho = .179). For voluntary laughter, the regression results indicated that age explained 19.09% of the variance ( $F(1,1032) = 243.467, p < .001, R^2 = .19$ , spearman's rho = -.345) (Fig. 4.22). For involuntary crying, age explained 5.22% of the variance in ratings ( $F(1,1032) = 56.815, p < .001, R^2 = .052$ , spearman's rho = .213). Finally, for involuntary crying, the results indicated that age explained 20% of the variance in ratings ( $F(1,1032) = 259.250, p < .001, R^2 = .20$ , spearman's rho = -.407) (Fig. 4.23).

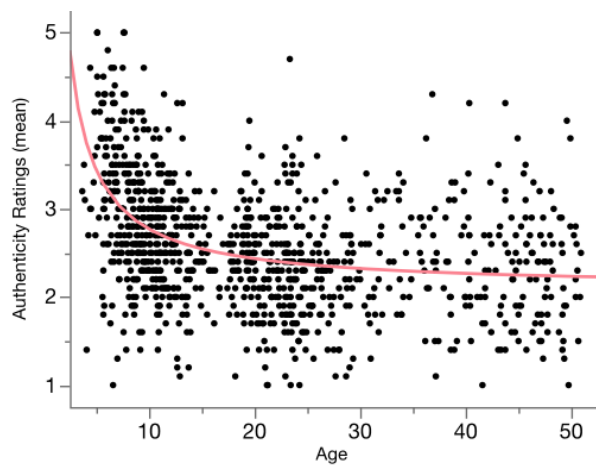
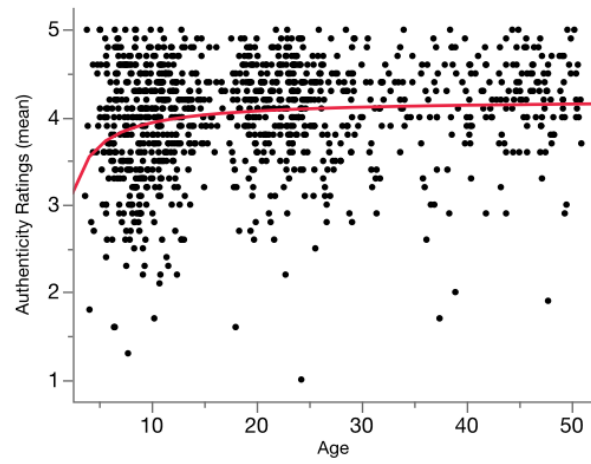


Figure 4.22 Mean ratings on authenticity scale for involuntary laughter (above) and voluntary laughter (below)

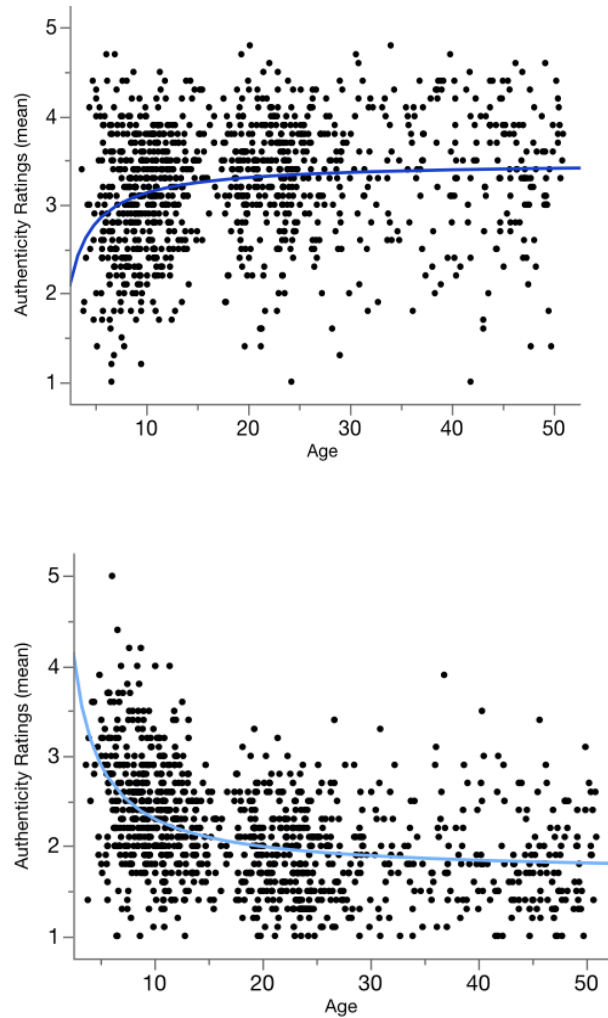


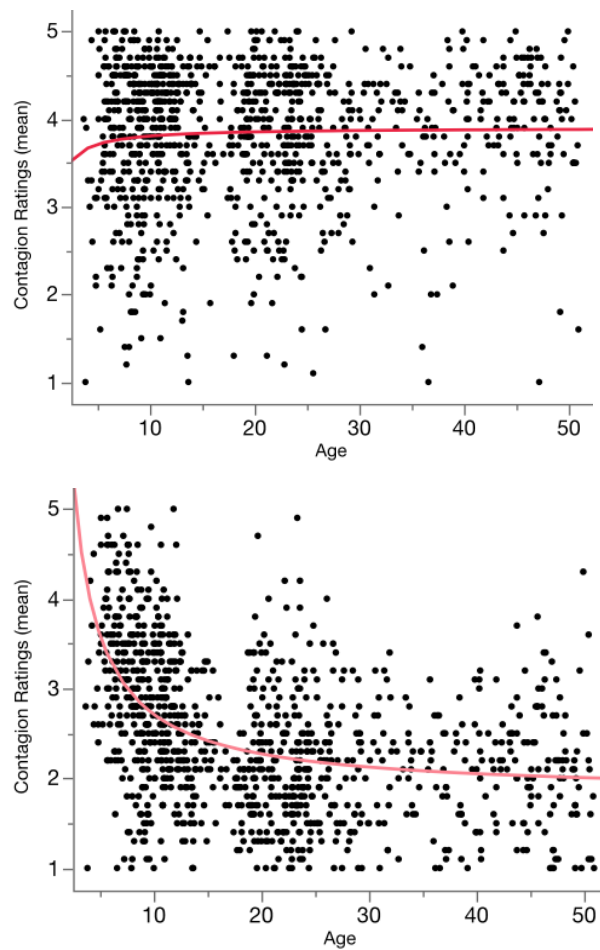
Figure 4.23 Mean ratings on authenticity scale for involuntary crying (above) and voluntary crying (below)

#### Contagion scale

For involuntary laughter, the results of the regression indicated that the predictor (age) did not explain any of the variance in ratings ( $F(1,1032) = 3.098, p = .078, R^2 = .00$ , spearman's rho = .025). For voluntary laughter, age explained 22.38% of the variance ( $F(1,1032) = 298.880, p < .001, R^2 = .22$ , spearman's rho = -.411) (Fig. 4.24). For involuntary crying, age explained 2.04% of the variance ( $F(1,1032) = 21.491, p < .001, R^2 = .020$ , spearman's rho = -.132). Finally, for involuntary crying, the results indicated that age explained 18.32% of the variance in ratings ( $F(1,1032) = 231.467, p < .001, R^2 = .18$ , spearman's rho = -.401) (Fig. 4.25).



In short, age predicted the rating performance of voluntary vocalisations better than that of involuntary vocalisations. The Spearman's rank correlation coefficients using a monotonic function to further assess the relationship between age and ratings of voluntary vocalisations and the relationship between age and ratings of involuntary vocalisations: the former correlation was found higher than the later one.



*Figure 4.24 Mean ratings on contagion scale for involuntary laughter (above) and voluntary laughter (below)*

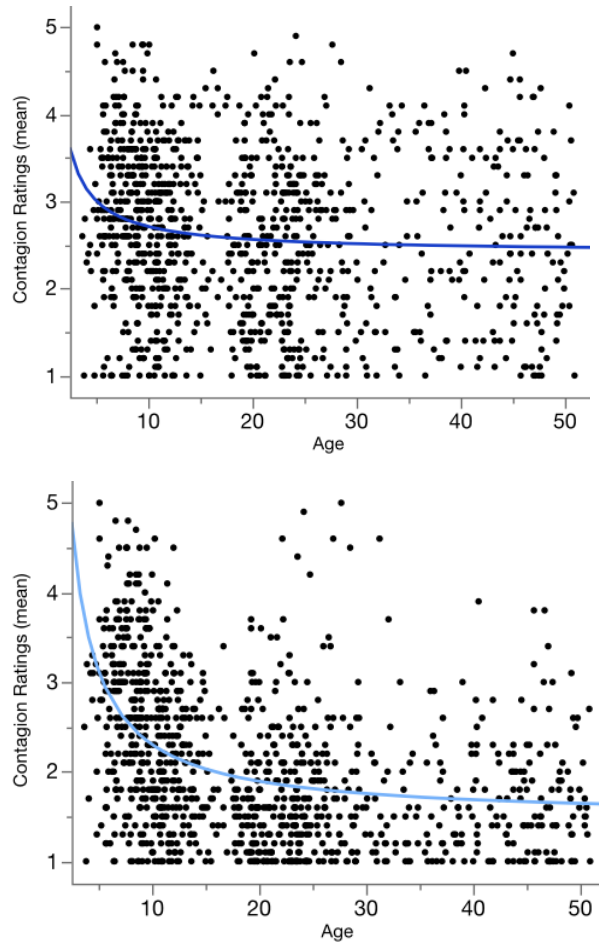


Figure 4.25 Mean ratings on contagion scale for involuntary crying (left) and voluntary crying (right)

#### 4.4 Discussion

The results of this experiment not only reveal age-related changes in the perception of laughter and crying, but also demonstrate that the perception of voluntary vocalisations differs from involuntary vocalisations through a slower developmental trajectory. These findings derive from the rating results on both authenticity and contagion scales.

The two rating scales to some extent seem to capture very similar properties of these emotional vocalisations. That is, if the sound is perceived as authentic, it can also be perceived as contagious, or vice versa. On both rating scales, I found robust main effects of involuntariness and emotions, and also observed significant interactions between these two within-subject factors. When comparing laughter to crying, and involuntary vocalisations to voluntary ones, laughing and involuntary vocalisations were consistently recognised as more authentic and more contagious. The relationship between perceived authenticity and contagiousness in laughter has been previously studied by McGettigan et al. (2015). In their study, evoked laughter (i.e., involuntary laughter) was rated as more authentic and more contagious than emitted laughter (i.e., voluntary laughter). The researchers further proposed that the perceived authenticity is modulated by sensorimotor areas, which showed greater activations in the participants who had better ability to differentiate involuntary laughter from voluntary laughter in a post-scanning categorisation task. However, the authors clarified that the sensorimotor engagement in the perception of laughter is not merely indicating a readiness to join in with laughter, but rather serves as a function to improve understanding of social signals - in this case, to enhance perceivers' ability to understand laughter by automatically engaging sensorimotor activations. The notion of dissociating the perceived authenticity and contagiousness of laughter is further supported by this experiment. In normal adults, the perception of authenticity and contagion show similar pattern (i.e., involuntary vocalisations are perceived as more contagious compared to voluntary vocalisations). By including participants of different ages, we are able to demonstrate that age effect has shown distinctively in the perception of authenticity and the perception of contagion.

### *Childhood and the perception of laughter*

The perceived authenticity of involuntary laughter showed a main effect of age, with children rating involuntary laughter as less authentic than did any other group. However, no age effect was found when the participants rated the contagiousness of involuntary laughter, signalling that the readiness to join in with involuntary laughter is observed throughout childhood to adulthood. The result can support the notion that joining involuntary laughter is an early developed ability. In contrast, the perception of authenticity can develop slower in childhood alongside with their cognitive ability is still developing. Children also rated voluntary laughter as more authentic than reported by any other group. Adolescents also perceived voluntary laughter as more authentic than did young adults, but this result was only marginally significant difference ( $p = .052$ ). Children again perceived voluntary laughter as more contagious than did any other age groups. No difference was found, however, between participants over 12 years of age and those later in adulthood. These findings of children's distinct performance from other age groups provide supportive evidence to previous findings that although children can recognise facial or vocal emotions above chance levels (Sauter et al., 2013), their performance improves with age. This pertains especially to the ability to recognise vocal emotions, which continues to develop after the age of 11 (Chronaki et al., 2014). However, it is worth mentioning that according to their perceived contagiousness of involuntary laughter, children between the ages of three and 11 have already demonstrated readiness to join in with laughter, which is no different than any other age group. This finding implies that the development of recognising involuntary laughter and responding with laughter can appear relatively early in childhood.

### *Adolescents and the perception of voluntary laughter*

As stated above, adolescents, like young adults and adults, exhibited less willingness to join in voluntary laughter than children. However, adolescents still perceived voluntary laughter as authentic to some extent. These results suggest that the ability to judge whether laughter is authentic may develop more slowly

than the ability to decide whether it is contagious. The difference between perceived authenticity and contagiousness in voluntary laughter may be due to the fact that to perceive contagiousness in laughter is a relatively early-developed process, as shown by participants of all ages rating involuntary laughter as contagious. On the other hand, to recognise authenticity in voluntary laughter involves the ability to infer the possible mental state of the speaker, which requires associated neural circuitry (i.e., medial prefrontal cortex) (McGettigan et al., 2015) that is still in development during adolescence (Blakemore & Mills, 2014; Gogtay et al., 2004; Mills, Lalonde, Clasen, Giedd, & Blakemore, 2014). Therefore, by highlighting the distinction between involuntary and voluntary laughter, our results provide empirical evidence to signify that the authenticity and contagiousness perception of voluntary laughter continues to develop before entering adulthood.

#### *Crying perceived as distinct from laughter on contagion but on authenticity scale*

The pattern of perceived authenticity of crying is similar to that of laughter. As expected, children performed distinctively from the other participants, rating involuntary crying as less authentic and voluntary crying as more authentic than did others. As in the comparison of voluntary laughter with involuntary laughter, the development of perceived authenticity in voluntary crying follows a slower trajectory when compared to involuntary crying. Adolescents rated voluntary crying as more authentic than did young adults and adults.

However, unlike involuntary laughter, which was highly contagious to participants across all ages, willingness to join in involuntary crying decreases over time. Children perceived crying, regardless of involuntariness, as more contagious than did young adults and adults. The perceived contagiousness in both involuntary crying and voluntary crying therefore continues to develop during adolescence. Furthermore, adolescents perceived the contagiousness of involuntary crying similarly to children; in other words, adolescents still perceived involuntary crying as contagious to some extent. The ability to mirror sadness by joining in remains during present adolescence, but this sensitivity to react to involuntary crying appears to decrease after adolescence. No difference in the perceived contagiousness of involuntary crying between adolescents, young

adults, and adults was found. There is a possible explanation for adolescents behaving similarly to children, who felt involuntary crying was contagious, but at the same time performing similarly to adults, who showed little readiness to join in involuntary crying. Adolescents may be acquiring displayed rules of expressing sadness during this transition time. Indeed, adolescents have been shown to develop great ability for regulating experienced sadness and controlling their expressions based on what reactions would be expected from the respondent (Zeman, Cassano, Perry-Parrish, & Stegall, 2006; Zeman & Shipman, 1997).

Our results also imply that compared to adults, adolescents remain sensitive to voluntary crying, and that the ability to perceive contagiousness from voluntary crying could continue to develop in early adulthood. This suggests that before the age of 30, the participants are to some extent growing in the capacity to mirror the emotion associated with crying sounds, even when they are produced voluntarily. This long-lasting developmental trajectory of perceiving voluntary crying has never before been reported. Although there is evidence that adult crying is considered to serve as a 'help-soliciting function' and that people are more willing to help a crying person than a non-crying person (Hendriks et al., 2008), there has been relatively little research previously conducted on the perception of adult crying. More empirical evidence is needed in the future, as understanding how we perceive adult crying can shed light on how we process sadness, which plays an important role throughout the lifetime.

## Chapter 5 Pupil responses to emotional vocalisations

### 5.1 Introduction

Pupil size variation has been used as an indication of emotion processing over the past 40 years. This methodology provides a window for exploring implicit physiological responses during the experience of different emotions (Darwin, Palli, & Sylvester, 1977; Hess, 1965; Hess & Polt, 1960; Leknes et al., 2013). Hess (1965) first proposed that pupil dilation may be associated with pleasant stimuli and that pupil constriction may be associated with unpleasant stimuli. In subsequent years, the relationship between pupillometry and emotion effects has been further addressed. One review (Janisse, 1973) argued that the dilation was driven by intensity of the stimulus and not its valence.

Studies on pupillary responses and emotion perception have further supported the notion of pupillary dilation as related to viewing arousing emotional pictures (Bradley, Miccoli, Escrig, & Lang, 2008) or to listening to arousing emotional sounds (Partala, Jokiniemi, & Surakka, 2000; Partala & Surakka, 2003). Bradley et al. (2008) used pleasant, unpleasant, and neutral pictures as stimuli to investigate underlying physiological responses while perceiving these emotional pictures. The pictures were selected from the International Affective Picture System (IAPS: Lang, Bradley, & Cuthbert, 2005) and matched with arousal ratings in the pleasant and unpleasant categories. The study found that pupils dilated in response to arousing stimuli but showed no significant difference between positive and negative pictures. Additionally, the pupillary dilation was found to covary with skin conductance changes. Similarly to the study summarized above, Partala & Surakka (2003) used pleasant sounds (e.g. a baby laughing), unpleasant sounds (e.g. a baby crying or a couple fighting),

and neutral sounds (e.g. regular office noise) as stimuli and again found that participants' pupil diameters only increased as a function of arousal but did not change because of the valence of stimuli.

Measuring pupil size has become a powerful method that is not only used for investigating emotion processing, but also as a marker in a wide range of studies to identify underlying physiological changes in human behaviour. For example, pupil dilation was found to be associated with cognitively effortful listening tasks and in general to be associated with a high processing load during task performance (Alnæs et al., 2014; Granholm & Steinhauer, 2004; Koelewijn, de Kluiver, Shinn-Cunningham, Zekveld, & Kramer, 2015; Zekveld, Heslenfeld, Johnsrude, Versfeld, & Kramer, 2014). Pupil dilation was also related to decision-making processes as pupil diameter increased either during decision formation process in the choice of 'YES' trials than in 'NO' trials (de Gee, Knapen, & Donner, 2014), or the pupillary dilation could correctly predict the timing of decisions (Einhäuser, Koch, & Carter, 2010). Moreover, in the learning process of decision making, pupil dilation has been found to signal uncertainty and surprise effects in gambling learning tasks (Lavín, San Martín, & Rosales Jubal, 2014; Preuschoff, Hart, & Einhäuser, 2011). In a study that lasted 16 training days in order for participants to learn a visual searching task, pupil dilation increased at the beginning of the training days but significantly decreased throughout the training process (Takeuchi, Puntous, Tuladhar, Yoshimoto, & Shirama, 2011). Pupil dilation, therefore, rather than only being an index of arousal perception in emotion studies, has been shown to be evidently associated with many other changes in humans' psychological state. The pupillary response indeed sheds light on different facets of the human mind, but a detailed mechanism between pupillary dilation, cognitive function and brain activation remains to be explored.

So far, there is evidence indicating that pupillary activity is closely related to the locus coeruleus (LC) embedded in a cortico-subcortical network, which is a small nucleus in the dorsal pons. The evidence was first established in monkeys and showed that changes of spiking activity in the LC closely aligned with changes of pupil sizes (Aston-Jones & Cohen, 2005; Costa & Rudebeck, 2016). Specifically, the spiking activity in the LC was observed to be greater prior to pupil dilation than during constriction (Joshi, Li, Kalwani, & Gold, 2016).



Moreover, the neural activities of some subcortical regions in monkeys, such as the colliculus and cingulate cortex – which is interconnected with the LC – were also involved in this LC-norepinephrine system (Joshi et al., 2016). An additional study directly measured blood-oxygen-level-dependent (BOLD) signals in the LC and investigated the relationship between the BOLD signals and pupil diameter in the human brain (Murphy, O’Connell, O’Sullivan, Robertson, & Balsters, 2014). The study identified that the continuous pupil diameter co-varied with BOLD activity in the LC while participants were performing an ‘oddball task’. The pupil diameter during task performance was also correlated with activity in the visual cortex, superior colliculus, bilateral thalamic nuclei, and anterior cingulate cortex, although the area did not survive for FDR-corrected multiple comparisons ( $p = 0.08$ ). The relationship between neural activity in the LC and pupillary response provided an early foundation for pupillometry studies and demonstrated that pupillary changes indeed correlate with brain activity although the underlying mechanism needs further investigation. With the advances in the temporal resolution of this technique, we were able to record the physiological responses while the participants were listening to emotional vocalisations.

In the current experiment, we were interested in the underlying pupillary responses when participants passively listened to emotional vocalisations without being aware of the differences of involuntariness among the stimuli. Specifically, the behavioural results from the previous experiment showed that the perceived authenticity of involuntary vocalisations was higher than voluntary vocalisations, and that crying sounds were also perceived as less authentic than laughter. The differences between involuntary and voluntary sounds in each expression was also found to be significantly different. To explore whether the differences we observed in the behavioural ratings are supported by the underlying physiological activity, we conducted a two-stage experiment to first record pupillary responses while participants passively listened to emotional vocalisations, and then record their behavioural ratings on these stimuli.

## 5.2 Methods

### 5.2.1 Emotional stimuli

There were 20 stimuli in each of the four conditions: involuntary laughter (IL), voluntary laughter (VL), involuntary crying (IC), and voluntary crying (VC) (see Chapter 2 for more details).

### 5.2.2 Participants

Forty-eight healthy native British English speakers volunteered to participate in this experiment (age range = 19-40 years; 28 females). All of them had normal or corrected-to-normal vision and reported no history of neurological or psychiatric illnesses.

All participants were paid £10 per hour for their time, and the project was approved by the UCL Research Committee.

### 5.2.3 Procedure

#### *Pupillometry task*

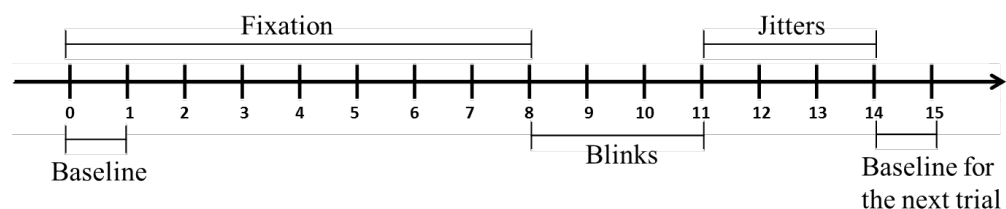
Participants were first introduced to the testing room and seated on a non-adjustable chair. They were told that they would be listening to different types of emotional sounds and that their pupil diameter would be recorded throughout the task. They were not informed that the study was about authenticity processing in laughter and crying. The sounds were presented via headphones and an adjusted chinrest was used to minimize head movements and to keep participants' eyes at a distance of 65cm from the centre of the computer screen.

The task included 80 stimuli in total, which were divided into four blocks. Each block consisted of 20 trials using either laughter or crying stimuli. Half of the 20 trials were voluntary vocalisations and the other half were involuntary vocalisations. For the first laughter block, the 10 trials of each condition (i.e., IL and VL) were first randomly selected, and then the other 10 trials of each condition were assigned to the second laughter block. For crying blocks, the

procedure was performed as the same as in the laughter blocks. Stimuli were presented in a randomized order within blocks, and the order of the blocks was counterbalanced across participants. Short breaks were allowed between blocks to minimize fatigue.

A nine-point calibration for eye movements was performed before each block. Participants were then instructed to listen carefully to each sound while keeping their eyes open and looking at the fixation point (a cross) on the centre of the screen. In each trial, the fixation point was first presented for one second in which no task-related processing occurred, and then the fixation point remained on the screen during the sound presentation (average duration = 2.51 seconds, SD = 0.36) and for four seconds after the offset of the sound, when it was replaced by an asterisk. The trial structure is illustrated in Figure 1. Participants were told that they could blink and relax when the asterisk was on the screen (three seconds). The inter-trial interval randomly ranged between 0 and 3 seconds to reduce possible expectation effects regarding the onset of the following trial. The lighting of the testing room was kept at a constant level for all participants.

Participants' pupil diameters were recorded using the High-Speed Video Eye Tracker Toolbox (HS-VET, Cambridge Research Systems Ltd.). The sampling rate was 250Hz. Auditory stimulus presentation was controlled using Matlab on a desktop PC computer and delivered through headphones to participants using the psychophysics toolbox (version R2010a and R2012b, Mathworks, Sherborn, MA, USA). Emotional vocalisations were played through high-quality headphones (Sennheiser Professional HD 25-II).



*Figure 5.1 Trial structure*

### *Behavioural task*

After completing the pupillometry task, participants completed a behavioural perception task. They rated each vocalisation on two different 7-point Likert scales: authenticity and arousal. For the authenticity ratings, participants rated the extent to which the emotional sound reflected a genuinely-felt emotion ('Does the sound reflect a genuinely felt emotion?' One signified posed: the speaker was not feeling the emotion, and seven signified genuine: the speaker was genuinely feeling the emotion). For arousal ratings, participants rated the level of arousal of the speaker ('Arousal: does the sound reflect low or high arousal?' One signified low arousal: the person is feeling sleepy and with no energy, and seven signified high arousal: the person is feeling alert and energetic). The two rating scales corresponded to two separate blocks; the full set of vocalisations was presented in a randomized order in each block and the order of the blocks was counterbalanced over the participants. This task lasted approximately 20 minutes.

## 5.2.4 Data analysis

### 5.2.4.1 Pupillometry data

Due to their eye make-up, low eyelid or machine malfunction, eight participants recorded less than 70% of their total data and were therefore excluded. Pupil diameter data for each participant were pre-processed using Matlab (R2013b). The mean and SD of the pupil diameter were calculated for each pupil trace, during a time period starting one second before the stimulus onset and ending three seconds after the stimulus offset (total seven seconds). For each trace, zero values and diameter values that were three SD's below the mean diameters were coded as blinks. Traces containing more than 15% of blinks (1.4 seconds) were excluded from the analyses (Koelewijn et al., 2015). The baseline pupil diameter was defined as the pupil size in the one-second interval preceding stimulus onset. To ensure that we had reliable baseline measures, pupil traces containing more than 40% of blinks during the baseline were excluded. After these quality checks, eight additional participants were excluded because after screening they had less than half of the trials left (i.e., < 10) in one or more of the conditions (Nuske, Vivanti, Hudry, & Dissanayake, 2014). The 32 participants (age 19-35, mean age

= 24.87, SD = 4.52, 17 females) included in the analyses had usable data for at least 50% of the trials in each condition (on average 91%; SD = 0.18; range = 55-100%). To remove extreme sample-to-sample changes in pupil diameter due to partial eyelid closures on either side of blinks, samples deviating more than two SD's from the mean pupil diameter within 350ms were removed, and these gaps were linearly interpolated (Nuske et al., 2014). All remaining traces were baseline-corrected by using the mean pupil size within the one-second period prior to the onset of the stimuli as a baseline value for each trace, and then subtracting the baseline value from the value for each time point within the trace. These baseline-corrected pupil diameters were averaged over the trials according to the stimulus categories for each participant, and were then analysed with repeated-measures analyses of variance (ANOVA). Greenhouse-Geisser corrections were applied when necessary (Mauchly's sphericity test).

#### 5.2.4.2 Behavioural data

Repeated-measures ANOVAs were conducted separately for authenticity and arousal responses, with expression (laughter/crying) and involuntariness (involuntary/voluntary) as within-subject factors. Significant interactions were then analysed by using paired samples t-tests to compare the difference between ratings of involuntary and voluntary vocalisations in laughter or crying conditions.

## 5.3 Results

### 5.3.1 Behavioural results

Participants' authenticity responses to laughter and crying are presented in Figure 5.1.1. As expected, involuntary vocalisations ( $M = 5.02$ ,  $SD = 0.60$ ) were perceived as more authentic than voluntary vocalisations ( $M = 2.77$ ,  $SD = 0.47$ ; main effect of authenticity ( $F[1,29] = 233.694$ ,  $MSE = 0.654$ ,  $p < .001$ ,  $\eta_p^2 = .890$ ). The main effect of expression was also significant, indicating that laughter ( $M = 4.29$ ,  $SD = 0.48$ ) was generally rated as more authentic than crying ( $M = 3.50$ ,  $SD = 0.46$ ;  $F[1, 29] = 47.611$ ,  $MSE = 0.386$ ,  $p < .001$ ,  $\eta_p^2 = .621$ ). The interaction between expression and involuntariness exhibited a marginally significant difference ( $F[1, 29] = 4.119$ ,  $MSE = 0.099$ ,  $p = .052$ ,  $\eta_p^2 = .124$ ) (Fig. 5.2).

Regarding arousal, involuntary vocalisations ( $M = 4.91$ ,  $SD = 0.58$ ) were rated more highly than voluntary vocalisations ( $M = 3.51$ ,  $SD = 0.55$ ; main effect of involuntariness,  $F[1,29] = 150.146$ ,  $MSE = .393$ ,  $p < .001$ ,  $\eta_p^2 = .838$ ), indicating that involuntary vocalisations were perceived as sounding more aroused than voluntary ones. The main effect of expression was also significant ( $F[1,29] = 154.341$ ,  $MSE = .419$ ,  $p < .001$ ,  $\eta_p^2 = .842$ ), demonstrating that laughter ( $M = 4.94$ ,  $SD = 0.57$ ) was generally perceived as sounding more aroused than crying ( $M = 3.48$ ,  $SD = 0.58$ ). Additionally, the interaction between expression and involuntariness was significant ( $F[1,29] = 52.527$ ,  $MSE = .141$ ,  $p < .001$ ,  $\eta_p^2 = .644$ ) (Fig. 5.3). Follow-up paired-sample t-tests showed that the effect of involuntariness on perceived arousal was larger for laughter (involuntary laughter:  $M = 5.89$ ,  $SD = 0.61$ ; voluntary laughter:  $M = 3.99$ ,  $SD = 0.72$ ;  $t(29) = 14.89$ ,  $p < .001$ ) than for crying (involuntary crying:  $M = 3.93$ ,  $SD = 0.79$ ; voluntary crying:  $M = 3.02$ ,  $SD = 0.58$ ,  $t(29) = 6.51$ ,  $p < .001$ ). Involuntary crying and voluntary laughter had similar arousal levels ( $t(29)=3.48$ ,  $p = 0.73$ ), whereas all the other conditions differed significantly from each other ( $p < .001$ ).

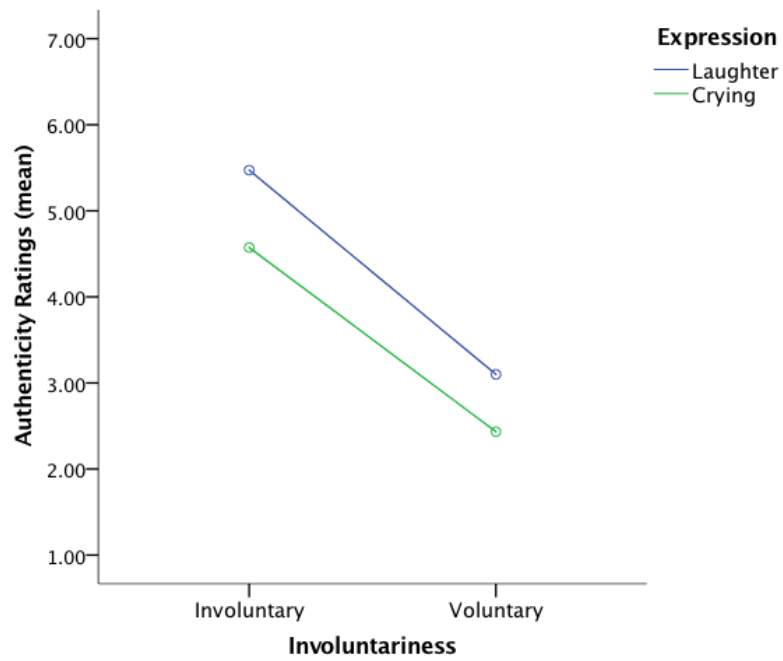


Figure 5.2 Results of authenticity ratings (on 7-point Likert Scale) from 30 participants

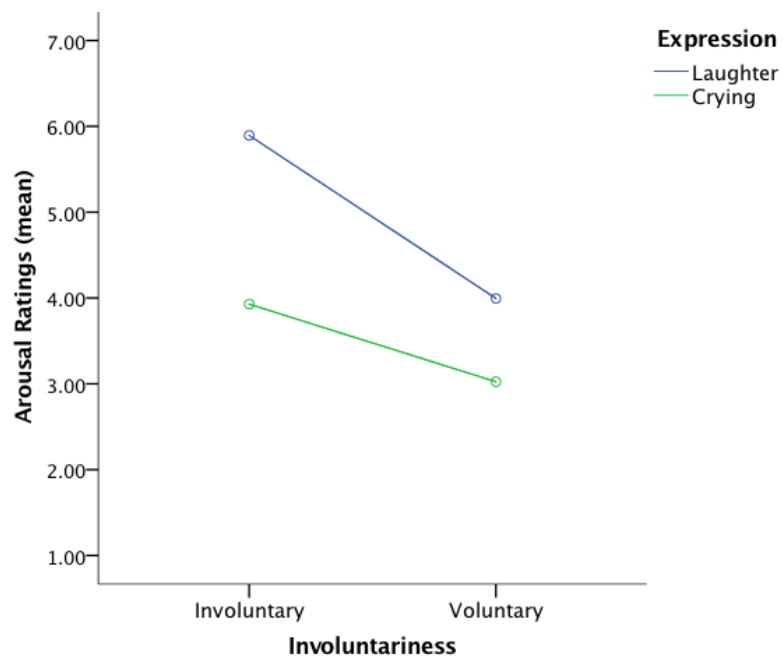


Figure 5.3 Results of arousal ratings (on 7-point Likert Scale) from 30 participants

### 5.3.2 Pupillometry results

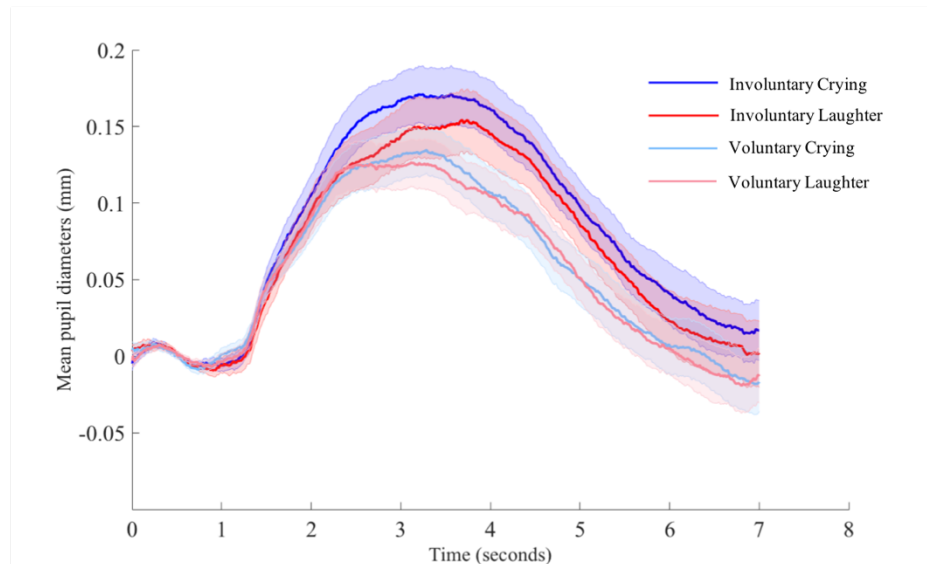
The average pupil responses for each condition are shown in Figure 5.4. The average pupil dilation was 0.076 mm (SD = 0.07), and the average stimulus-induced pupil dilation during sound presentation (around three seconds) was 0.102 mm (SD = 0.07). After the stimulus onset (from 1s on the timeline), there was no obvious pupil dilation during the first 500ms, followed by a steep increase in the pupil size observed across all conditions. Peak dilation was reached at around 2-to-3 seconds after stimulus onset (3-to-4 seconds after the onset of the trial), and this was followed by pupil constrictions lasting for 3-to-4 seconds depending on conditions: the pupil responses for voluntary vocalisations constricted earlier than for involuntary vocalisations.

A 2x2 ANOVA was conducted with expression (laughter/crying) and involuntariness (involuntary/voluntary) on mean pupil dilation during full trials (i.e., from the stimulus onset to 3 seconds after the stimulus offset, or 6 seconds in total). The ANOVA showed a main effect of involuntariness ( $F[1,31] = 13.686$ ,  $MSE = .002$ ,  $p = .001$ ,  $\eta_p^2 = .306$ ), indicating that pupils dilated more for involuntary vocalisations ( $M = 0.089$ ,  $SD = 0.078$ ) than for voluntary vocalisations ( $M = 0.063$ ,  $SD = 0.066$ ). There was no significant main effect of expression ( $F[1,31] = 1.363$ ,  $MSE = .002$ ,  $p = .252$ ,  $\eta_p^2 = .042$ ), signalling that there was no significant difference between pupil dilation for laughter ( $M = 0.072$ ,  $SD = 0.074$ ) and for crying ( $M = 0.081$ ,  $SD = 0.070$ ). No significant interaction was found between involuntariness and expression ( $F(1,31) = .910$ ,  $MSE = .001$ ,  $p = .347$ ,  $\eta_p^2 = .029$ ) (Fig. 5.5).

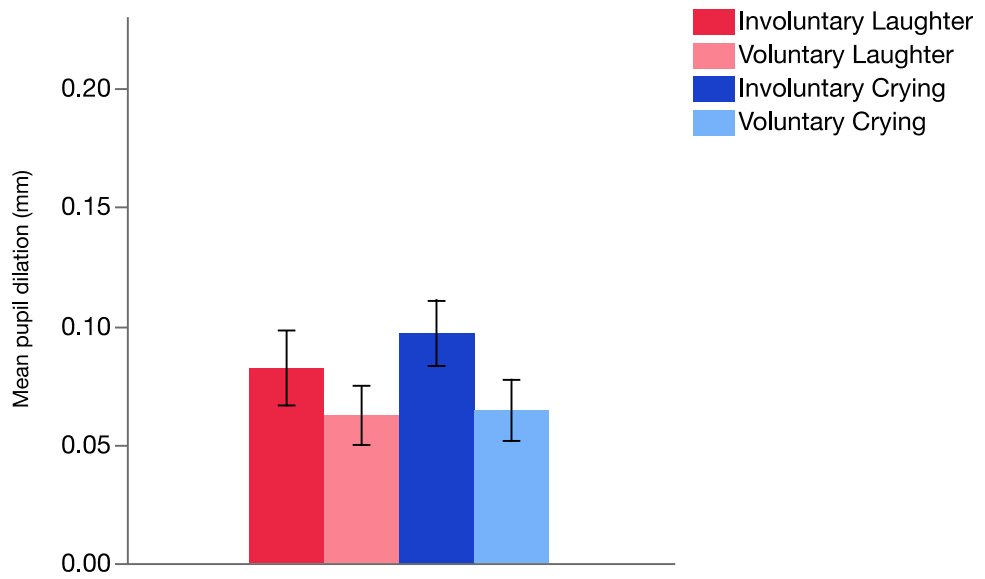
Two 2x2 ANOVAs were also conducted on specific indexes: the mean pupil diameter during the stimulus presentation (i.e., 3 seconds after the onset of stimulus) and the peak dilation (i.e., the maximum diameter throughout the trials) (Fig. 5.6, 5.7). The ANOVAs both showed significant main effects of involuntariness (mean:  $F[1,31] = 8.256$ ,  $MSE = .01$ ,  $p = .007$ ,  $\eta_p^2 = .210$ ; peak:  $F[1,31] = 12.616$ ,  $MSE = .002$ ,  $p = .001$ ,  $\eta_p^2 = .289$ ) indicating that pupils dilated more for involuntary vocalisations than for voluntary ones. There was no significant main effect of expression (mean:  $F[1,31] = 1.378$ ,  $MSE = .002$ ,  $p = .249$ ,  $\eta_p^2 = .043$ ; peak:  $F[1,31] = .876$ ,  $MSE = .003$ ,  $p = .357$ ,  $\eta_p^2 = .027$ ) showing



that pupil responses did not differ for laughter and for crying. No significant interaction was found (mean:  $F[1,31] = 1.184$ ,  $MSE = .001$ ,  $p = .285$ ,  $\eta_p^2 = .037$ ; peak:  $F[1,31] = 1.392$ ,  $MSE = .002$ ,  $p = .247$ ,  $\eta_p^2 = .043$ ) (Fig. 5.7). A 2x2 ANOVA on pupil baseline showed no significant effect of expression ( $F[1,31] = .170$ ,  $MSE = .297$ ,  $p = .683$ ,  $\eta_p^2 = .005$ ), involuntariness ( $F[1,31] = .448$ ,  $MSE = .014$ ,  $p = .508$ ,  $\eta_p^2 = .014$ ), or interaction ( $F[1,31] = .495$ ,  $MSE = .006$ ,  $p = .487$ ,  $\eta_p^2 = .016$ ), which indicates that the mean pupil diameters in the baseline durations were stable for the four conditions (Fig. 5.8).

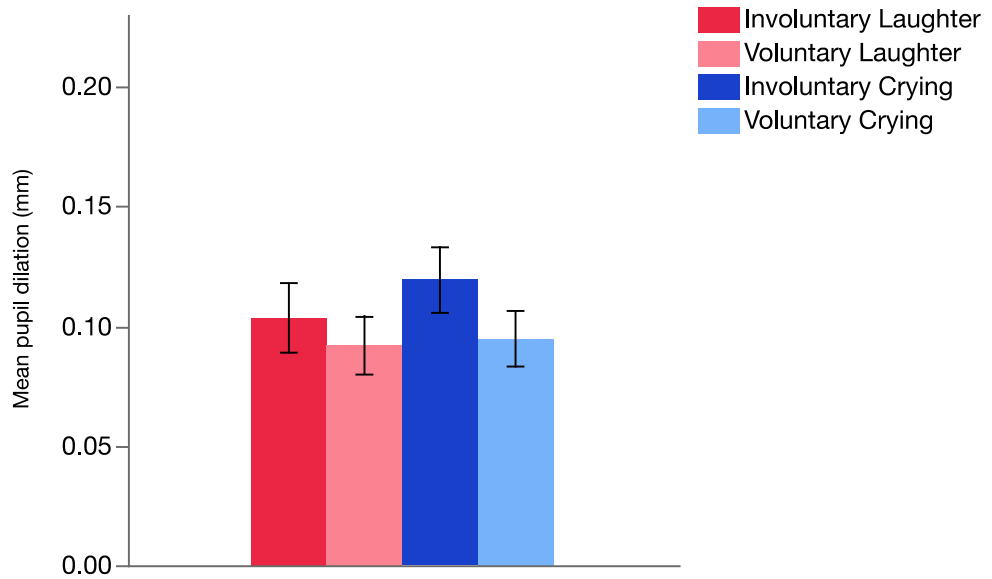


*Figure 5.4 Average pupil responses for each condition*



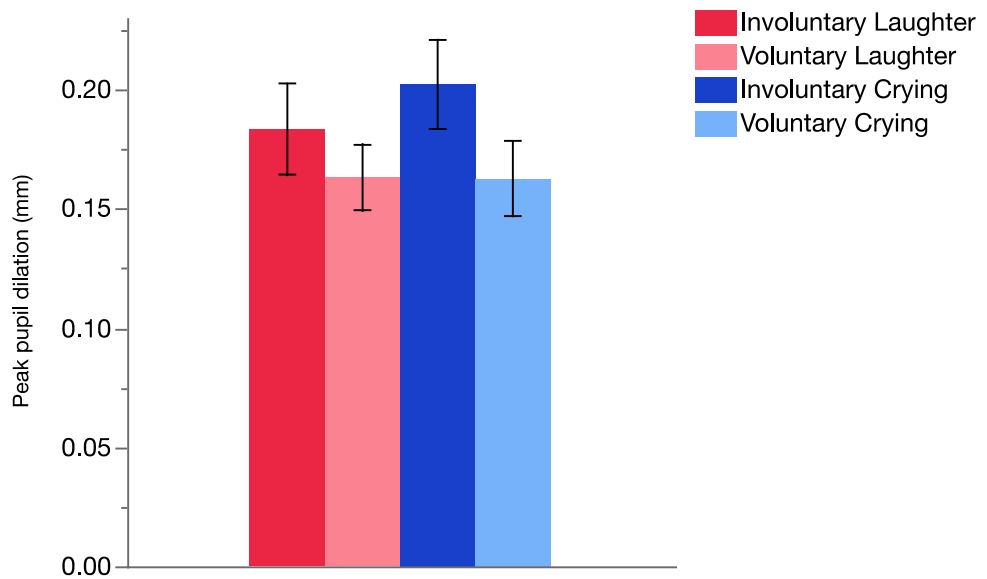
*Figure 5.5 Mean pupil dilation over trials for each condition*

The time window over which the mean pupil dilation was computed corresponds to the range between 1 s to 7s (i.e., 6 seconds in total). Error bars indicate the standard error of the mean.

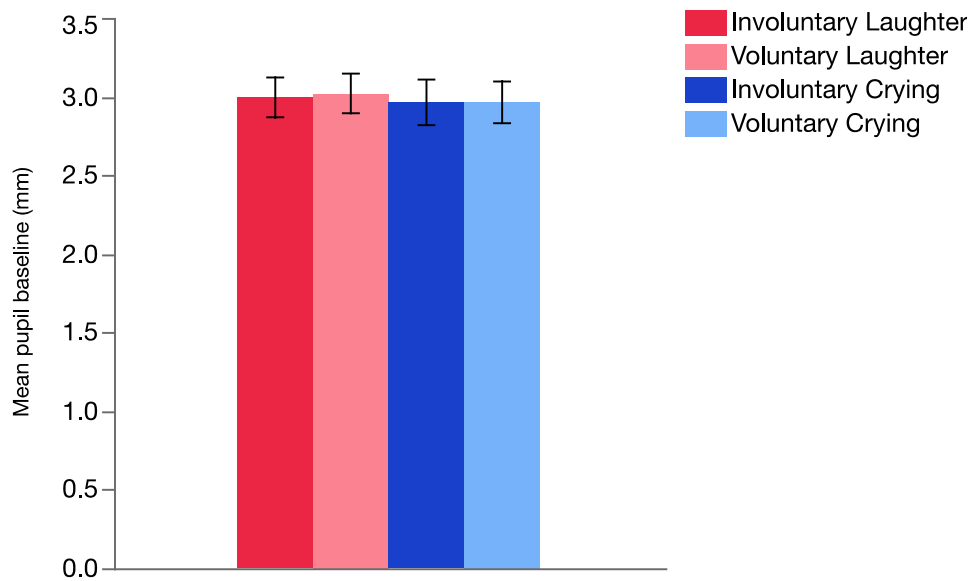


*Figure 5.6 Mean pupil dilation of duration of sound presentation.*

The time window over which the mean pupil dilation was computed corresponds to the range between the 1 second and 4 seconds (i.e., duration of sound presentation). Error bars indicate the standard error of the mean.



*Figure 5.7 Average peak pupil dilation across participants*



*Figure 5.8 Average baseline pupil diameters across participants*

#### 5.4 Discussion

The main finding in this experiment was that pupillary responses for involuntary vocalisations were significantly greater than for voluntary vocalisations regardless of expression. Although participants explicitly rated adults' crying as less authentic than laughter, their pupillary responses were only modulated by the difference between involuntary and voluntary vocalisations, and not by expression.

Several previous studies have found that when participants perceive a stimulus with a strong affect, their pupil diameters increase with the extent of intensity of the stimulus regardless of its modality (e.g. visual or auditory stimuli) or contents (e.g. male or female) (Bradley et al., 2008; Janisse, 1973; Partala et al., 2000; Partala & Surakka, 2003). Our results were consistent with these findings (Bradley et al., 2008; Partala et al., 2000; Partala & Surakka, 2003). Involuntary laughter and involuntary crying, which have higher arousal and authenticity levels, induced greater pupil dilation than did voluntary laughter and crying. However, the pupillary responses in our experiment were not completely consistent with the rating results. Participants rated laughter as more authentic than crying, and

rated the speakers who had produced laughter as sounding more aroused than those who had produced crying. In addition, we found that the interaction of arousal ratings between expression and involuntariness was significant, which indicates that the perceived arousal difference between involuntary and voluntary laughter was greater than the perceived difference between involuntary and voluntary crying. The behavioural results stated above however were not reflected in pupillary results. The pupillary results indeed provide physiological evidence on the perceived differences between involuntary and voluntary vocalisations in arousal and authenticity ratings, but it also demonstrates a discrepancy between implicit perception and explicit ratings on these emotional vocalisations.

The size of the pupil is controlled by two smooth muscles of the eye, which makes it very difficult to control pupillary dilation by voluntary efforts. Although it may be possible to dilate pupils by internally picturing highly arousing events or pictures, it is impossible to voluntarily inhibit pupil dilation (Laeng, Sirois, & Gredeback, 2012). In the current experiment, the greater pupil dilation for involuntary vocalisations than for voluntary vocalisations suggests that only listening to emotional sounds without consciously knowing anything about involuntariness can induce spontaneous information processing in response to involuntary vocalisations. Pupillometry has been used in previous studies as an indicator to unveil subliminal information processing (Leknes et al., 2013; Nuske et al., 2014). Nuske et al. (2014) studied emotion processing in two groups of participants – autistic and typically developing (TD) children – by subliminally (non-consciously) or supraliminally (consciously) presenting fearful or neutral faces while recording their pupil sizes. The study showed that pupillary responses were significantly different between the two groups in the non-conscious conditions, but not different in the conscious conditions. Specifically, in the non-conscious condition, the peak amplitude of pupil sizes of TD children was significantly greater in duration when viewing the fearful faces than the neutral faces. Meanwhile, the peak amplitude of autistic children was greater when viewing the neutral faces rather than the fearful faces. The authors therefore argued that emotion processing is fundamentally different in autistic children, characterized by reduced unconscious emotional reactivity and the requirement of consciousness involvements. In the current experiment, it is

possible that pupil dilated significantly greater for involuntary sounds than for voluntary sounds implying involuntary vocalisations were processed differently from voluntary vocalisations.

There is converging evidence indicating that pupillary responses are effective indices of 'hidden' emotion processing (Laeng et al., 2013, 2012; Leknes et al., 2013). In previous studies, 'hybrid' faces were created by combining a high-pass filtered neutral face with a low-pass filtered emotional face. Participants were not aware of that these hybrid faces contained emotional information by judging these faces as neutral. On the other hand, hybrid faces were perceived as less friendly if a negative but a positive emotional face was embedded in a neutral face. In line with friendliness rating results, pupillary response to the negative hybrid faces were greater than to real neutral faces and to the positive hybrid faces. These studies showed that pupil diameters changed greatly for invisible emotions which participants would not be able to consciously recognise. Although in the current experiment participants were aware of the difference between involuntary vocalisations and voluntary vocalisations, they performed poorly on recognising authenticity carried in crying sounds. The pupillary response showed that the participants perceived the difference between involuntary crying from voluntary crying, however their authenticity ratings on crying were possibly affected by other reasons, for example, display rules.

One explanation for the lack of a main effect of expression observed in the behavioural ratings on pupil dilation is that human pupils do not react specifically to different emotions: rather, our pupils simply react to arousing stimuli (Partala et al., 2000; Partala & Surakka, 2003). However, this explanation is not consistent with that the involuntary crying was sounding no more aroused than voluntary laughter, but pupil significantly dilated for perceiving involuntary crying sounds than for voluntary laughter. Another possible explanation is that our pupils strongly react to involuntary laughter and crying because these two kinds of stimuli carry more 'intense' emotional information than do voluntary stimuli. However, there is evidence showing that pupils constrict rather than dilate in response to photographs of sad faces, which are rated as more intense than others (Harrison, Singer, Rotshtein, Dolan, & Critchley, 2006; Harrison, Wilson, & Critchley, 2007). In these studies, the pupil size of one face on a photograph was photoshopped into 64, 80, 100, and 180% of the original size

without participants' awareness. Participants were asked to look at photographs of happy, sad, angry, and neutral faces. Only photographs of sad faces with smaller pupils were rated significantly more negative and more intense than those with larger pupils. This pupillary contagion of sad faces was supported by related activation in the mid-brain and the right angular gyrus, which are suggested to be involved in social cognition (Harrison et al., 2006). The researchers proposed that the effect was a specific phenomenon that occurs when perceiving sadness from facial expression. This suggests that autonomic activation plays a role in perceiving sadness through facial expression.

The reported pupillary constriction when perceiving sad faces is inconsistent with our results, in which participants exhibited greater pupil dilation in response to involuntary crying. As there are no other studies investigating pupil reactivity to sad stimuli of both visual and auditory modalities on healthy adults, it is still unclear whether perceiving involuntary vocalisations with greater pupillary dilation indicates an automatic activation response to the intensity of the stimuli.

## Chapter 6 The neural correlates underlying the perception of laughter and crying

### 6.1 Introduction

There has been a long history of investigating pathological laughing and crying (PLC) since the 19<sup>th</sup> century. As reviewed in Chapter 1, lesions along the corticobulbar and corticospinal tracts were identified to be associated with PLC, showing both cortical and subcortical contributions to the syndrome. However, when comparing the impaired cortical and subcortical involvements in the pure form of pathological laughing (PL) and pathological crying (PC), more cortical regions seem to be identified in the PL than in the PC. However, PC patients with epileptic seizures to some extent exhibited cortical abnormalities in the temporal and frontal lobes, and PL patients caused by seizures were found to have abnormal neural activity in the cingulate gyri, while PLC epileptic patients were found to show abnormal neural activity in the orbito-cingulate region (Kahane et al., 2003). The pathological laughter is suggested to occur when the two systems of expressing laughter were partially impaired (Wild, Rodden, Grodd, & Ruch, 2003). Specifically, evoked laughter and crying can be triggered through the 'emotionally driven' system (i.e., involuntary system), and the system is modulated by the 'voluntary' system which can inhibit emotionally driven inappropriate laughter or crying. From this point of view, pathological laughter or crying occurs when the voluntary system release to suppression to the expression (Lauterbach et al., 2013; Wild et al., 2003).

The areas identified in a paper by Lauterbach et al. (2013) on PLC and emotional liability research involved several motor- and emotion-associated brain regions which were proposed to be underlying neural correlates of the two



systems. For the voluntary system, the majority of motor related cortical areas were identified, such as the primary motor cortex, premotor cortex, supplementary motor cortex (SMA), pre-SMA, somatosensory cortex, and supramarginal gyrus. For the emotionally driven system, subcortical and cortical regions were identified involving the anterior cingulate gyri, orbitofrontal cortex, inferior temporal gyri, occipitotemporal gyrus, parahippocampal gyrus, anterior insula, and related temporal cortices. The cortical regions in the voluntary system then sends signals to the pons, and the emotionally driven system sends signals to the amygdala, hypothalamus, and then to the periaqueductal gray (PAG) (Lauterbach et al., 2013). The former system is proposed to serve the function of intentionally producing laughter and/or crying, and the latter is suggested to be responsible for producing laughter and crying triggered by internal or external stimulation.

The extensive review on pathological laughter and crying indeed sheds lights on plausible neural circuits underlying the production of laughter and crying, yet only little empirical research has focused on the production of laughing and crying with normal participants. One study investigated the production of laughter and revealed involvements of the lateral sensorimotor areas identified in the conditions of producing voluntary laughter and producing tickling laughter, however, the area increased activations when the participants were asked to inhibit the tickling laughter (Wattendorf et al., 2013). It can indicate that the role of the lateral sensorimotor system is not limited to suppressing uncontrolled laughter, but rather it can also be involved in a general underlying neural mechanism of producing laughter. In accordance with the two systems delineated by Lauterbach et al. (2013), the regions identified by Wattendorf et al. (2013) partly overlapping with the emotionally driven system (i.e., amygdala, hypothalamus, PAG) can confirm that the system is indeed reactive to external physical stimulation and engages in the production of involuntary laughter.

This distinctive pattern of brain activations identified in perceiving involuntary and voluntary laughter was recently investigated in a study by McGettigan et al. (2015). By passively listening to these two kinds of laughter, the sensorimotor cortices showed increased involvement positively correlated with participants' ability to discriminate 'real' laughter from 'posed' laughter according

to the perceived authenticity in involuntary and voluntary laughter. In addition, neural activation in the anterior medial prefrontal cortex (amPFC) was found to be significantly engaged in perceiving voluntary laughter rather than perceiving involuntary laughter, which suggested that the listeners might be inferring laughers' intentions while encountering social laughter (McGettigan et al., 2015). In line with these findings, a later study further supported this notion by showing that activations in the amPFC were negatively correlated with perceived valence and authenticity of laughter. In contrast, activity in bilateral auditory cortices were positively correlated with the degree of valence, arousal, and authenticity perceived in laughter. In the same study, the right STG was further identified to be strongly associated with the laughter of the highest authenticity rating (Lavan, Rankin, Lorking, Scott, & McGettigan, 2017). So far, the studies stated above have successfully provided empirical evidence that brain activation can be modulated by affective properties of voluntary and involuntary laughter. The areas identified are potential candidates for understanding the functional neural correlates underlying the perception of other emotional vocalisations, such as voluntary and involuntary crying.

The previous two experiments show that perceived authenticity concerning laughter and crying may follow similar developmental trajectories. However, the authenticity ratings of voluntary vocalisations were shown to improve through early adulthood regardless of emotions. I also observed that the perceived contagiousness of laughter and crying showed distinct patterns regarding the involuntary vocalisations. Specifically, participants across all ages exhibited willingness to join in involuntary laughter, but only children reported that perceiving involuntary crying is contagious to some extent, and the willingness to join in involuntary crying decreased over time. Regarding the perceived contagiousness of the voluntary vocalisations, a slower developmental learning process was observed in crying than in laughter.

The aim of the current experiment is to delineate the neural systems implicated in the perception of laughter and crying, and how this is modulated by authenticity. This will enable us to determine whether the responses seen to voluntary and involuntary laughter in the previous study (McGettigan et al, 2015) were specific to laughter, or to the authenticity of any emotion.

## 6.2 Methods

### 6.2.1 Emotional Stimuli

Twenty tokens were selected for each condition: involuntary laughter, voluntary laughter, involuntary crying, voluntary crying (i.e., 80 in total). See Material Preparation Section. Another 20 tokens of emotional vocalisations including 6 tokens of disgust sounds, 7 tokens of contentment sounds, and 7 tokens of relief sounds were included in the experiment as a distractor condition to distract the participants from detecting the main experimental manipulations in the imaging study.

### 6.2.2 Participants

Twenty-four healthy native English speakers volunteered to participate in this experiment (age range = 18-48, Mean age = 24.75 years, SD = 6.95, fourteen females). All of them had normal hearing and vision or corrected-to-normal vision. No participants reported a history of neurological or psychiatric illnesses. The study was approved by the UCL Research Ethics Committee. They were paid £10 per hour for their time.

### 6.2.3 Design and procedure

Before going into the scanner, the participants were informed that they would be passively listening to emotional sounds for four sessions, and each session lasted for about 10 minutes. After the first two passive listening sessions, a structural scan would be performed, followed by the last two sessions of listening to emotional sounds. After the four sessions of the auditory phase of the experiment and the structural scan, there would be one session of emotional motor tasks, and the final session would be a theory of mind task. Participants were given clear instructions about the tasks and had time to practice before going to the scanner. Participants were not aware that the stimuli varied in terms of authenticity.

#### 6.2.4 Auditory sessions

Functional imaging data were acquired on a Siemens Avanto 1.5-Tesla MRI scanner (Siemens AG, Erlangen, Germany). Participants were informed that they would hear emotional sounds and some other types of sound and that they should listen carefully to the sounds.

Auditory presentation of emotional sounds took place in 4 runs of 65 echo-planar whole brain volumes (TR = 8.4s, TA = 3.4 s, TE = 50 ms, flip angle = 90°, 40 axial slices, 3 mm x 3 mm x 3 mm in-plane resolution). A sparse-sampling routine (Edmister et al., 1999; Hall et al., 1999) was employed, in which the auditory stimuli were presented in the quiet period between scans. Auditory onsets occurred 0.5 s (+- 0.5s jitter) before the beginning of the next whole-brain volume acquisition. Auditory stimuli were presented using MATLAB (version R2012b, Mathworks, Sherborn, MA, USA) and the psychophysics toolbox (Brainard 1997; Pelli 1997) via a Sony STR-DH510 digital AV control center (Sony, Basingstoke, UK) and MR-compatible insert earphones (Etymotic Research, Inc., Elk Grove Village, IL) worn by the participants.

All 100 stimuli (20 from each condition: voluntary/involuntary, laughter/crying; 20 from distract sounds: 6 disgust sounds, 7 relief sounds, 7 comfort sounds) were presented twice in total (once in each functional run). The condition order was pseudorandomized, with each auditory condition occurring once every 6 trials, including one trial of a Rest Baseline condition.

#### 6.2.5 Structural scan

After the first two sessions of listening to emotional sounds, high-resolution anatomical images were acquired using a T<sub>1</sub>-weighted magnetisation prepared rapid acquisition gradient echo sequence (repetition time = 2730 ms, echo time = 3.57 ms, flip angle = 7°, slice thickness = 1 mm, 160 sagittal slices, acquisition matrix = 256 × 224 × 160 mm, voxel size = 1 mm<sup>3</sup>).

### 6.2.6 Orofacial movement localizer (motor task)

After the auditory phase of the experiment, the listeners were informed that the next part would require that they move their facial muscles to mimic a happy face and a frowning face. During each trial of the motor condition, they were instructed to either 'SMILE' or 'FROWN'—or to 'REST' which required no facial movements. In the 'SMILE' condition, they were instructed to quickly initiate a voluntary smiling movement and then relax, continuing this movement until the instruction disappeared from the screen. In the 'FROWN' condition, they were instructed to move their eyebrows together and then relax, again continuing this movement until the instruction disappeared from the screen. Each trial lasted for 3.4 seconds. The condition order was pseudorandomized, with each condition occurring once every three trials.

A total of 110 echo-planar whole brain volumes (TR = 3.4s, TA = 3.4s, TE = 50 msec, flip angle = 90°, 40 axial slices, 3 mm x 3 mm x 3 mm in-plane resolution) were acquired during the task, in which the participants performed 30 trials in each condition. This session lasted for around five minutes.

### 6.2.7 Theory of mind localizer (TOM task)

Stimuli consisted of 10 stories in each of two conditions: (1) stories describing false belief (BELIEF) and (2) stories describing outdated (i.e., false) photographs and maps (PHOTO) (Saxe & Kanwisher, 2003). Both sets of stories required participants to represent false contents, while the critical difference was in the type of false content represented (i.e., a belief versus a photograph/map). Stories were followed by a true/false question that referred either to the situation in reality or to the false representation. There were an equal number of questions that referred to the reality and representation in each condition, and the order of conditions was pseudorandomized so that each condition occurred every two trials.

Every trial, a story was presented for 10 seconds followed by a true/false question lasting four seconds. Participants were asked to respond as quickly as possible. A total of 160 echo-planar whole brain volumes (TR = 3.4s, TA = 3.4s,

TE = 50 msec, flip angle = 90°, 40 axial slices, 3 mm x 3 mm x 3 mm in-plane resolution) were acquired during the task. This session lasted for around five minutes.

## 6.2.8 After scan

### 6.2.8.1 Behavioural Post-Test

After the scanning session was complete, the participants were asked to listen to each of the laughter/crying stimuli again and complete three behavioural tasks. The first task was to classify the items as 'real' or 'posed', and the following two tasks were to rate these stimuli using 7-point Likert scales on two parameters: Authenticity and Contagion. Their rating scales corresponded to separate blocks.

For the Authenticity ratings, participants rated the extent to which the emotional sound reflected a genuinely felt emotion ('Does the sound reflect a genuinely felt emotion?' 1 - posed, the speaker was not feeling the emotion; 7 - genuine, the speaker was genuinely feeling the emotion). Participants were informed that half the sounds were genuine and half were posed. For the Contagion ratings, participants rated the extent to which the sound is contagious ('To which extent is the sound contagious?' 1 - not at all, i.e., it does not make me feel like mimicking and/or feeling the emotion; 7 - very much, i.e., it makes me feel like mimicking and/or feeling the emotion).

### 6.2.8.2 Questionnaire

In the final part of the experiment, the participants were self-scored with three questionnaires used to see how the personality traits correlated with cerebral activity during the auditory phase of the experiment. These questionnaires were The Toronto Alexithymia Scale (TAS-20) (Bagby et al., 1992), The Emotional Contagion Scale (R. William Doherty, 1997), and The Questionnaire of Cognitive and Affective Empathy (The QCAE) (Reniers et al., 2010).

## 6.2.9 Data analysis

### 6.2.9.1 fMRI data analysis

Imaging pre-processing and analysis was performed with the SPM8 software package (Wellcome Trust Centre for Neuroimaging, London, UK, <http://www.fil.ion.ucl.ac.uk/spm>). Image pre-processing involved realignment of EPI images to remove the effect of head movement between scans, coregistration of the T1-weighted structural image to the mean EPI image, normalisation of EPI images into Montreal Neurological Institute (MNI) standard stereotactic space using normalization parameters derived from the coregistered T1-weighted image, and smoothing of normalised EPI images using a Gaussian kernel of 8mm FWHM. Analyses of imaging data were conducted using a random-effects model.

#### *Auditory Session*

At the single-subject level, event onsets from all 6 conditions (Involuntary Laughter (IL), Voluntary Laughter (VL), Involuntary Crying (IC), Voluntary Crying (VC), Distract Sounds, and Rest Baseline) were modelled as instantaneous and convolved with the canonical hemodynamic response function. Individual design matrices were constructed for each subject (All Laughter > Rest, All Crying > Rest, IL > VL, VL > IL, IC > VC, VC > IC), modelling each of the four experimental conditions in four scanning runs and including movement parameters derived from the realignment step as nuisance variables. These contrast images were entered into a second-level, 1-sample t-tests for the group analysis. Additional second-level regression models were also run for two of the contrasts (All Laughter > Rest and All Crying > Rest), with individual Cohen's d scores from the behavioural post-test and with individual questionnaire scores as covariates in each case.

### *Analyses of localizers*

*Orofacial movement localizer.* At the first level, event onsets from all three conditions (Smile, Frown, Rest) were modelled and convolved with a canonical hemodynamic response function. Individual design matrices were constructed for each subject (Smile+Frown > Rest), and the contrast image was entered into a second-level, 1-sample t-test for the group analysis. In the results of the contrast, all clusters ( $p < .005$ , uncorrected) were saved as a binary mask and then were used to identify the common activations which were also activated within the auditory sessions.

*Theory of mind task.* At the first level, event onsets from Belief and Photo conditions were modelled and convolved with the canonical hemodynamics response function. Individual design matrices were constructed for each subject (Belief > Photo), and the contrast image was entered into a second-level, 1-sample t-test for the group analysis. In the results of the contrast, all clusters ( $p < .005$ , uncorrected) were saved as a binary mask and then were used to identify the common activations which were also activated within the auditory sessions.

All results of the subtraction contrasts and of the regression analyses in the experiment are reported at an uncorrected voxel height threshold of  $p < 0.005$ . A cluster extent correction was applied for a whole-brain alpha of  $p < 0.001$  using a Monte Carlo simulation with 10,000 iterations implemented in MATLAB (Slotnick et al., 2003). This determined that an extent threshold of 68 voxels (where the probability curve approached 0) could be applied for the voxel height thresholds of  $p < 0.005$ . The anatomical locations of significant clusters (at least 8mm apart) were labelled using the SPM Anatomy Toolbox (version 22C; Eickhoff et al., 2005).

#### 6.2.9.2 Behavioural data analysis

Repeated-measures ANOVAs were conducted separately for authenticity and contagion responses, including expression (laughter/crying) and involuntariness (involuntary/voluntary) as within-subject factors. The results of significant interactions were followed by simple t-tests on ratings of expression and on

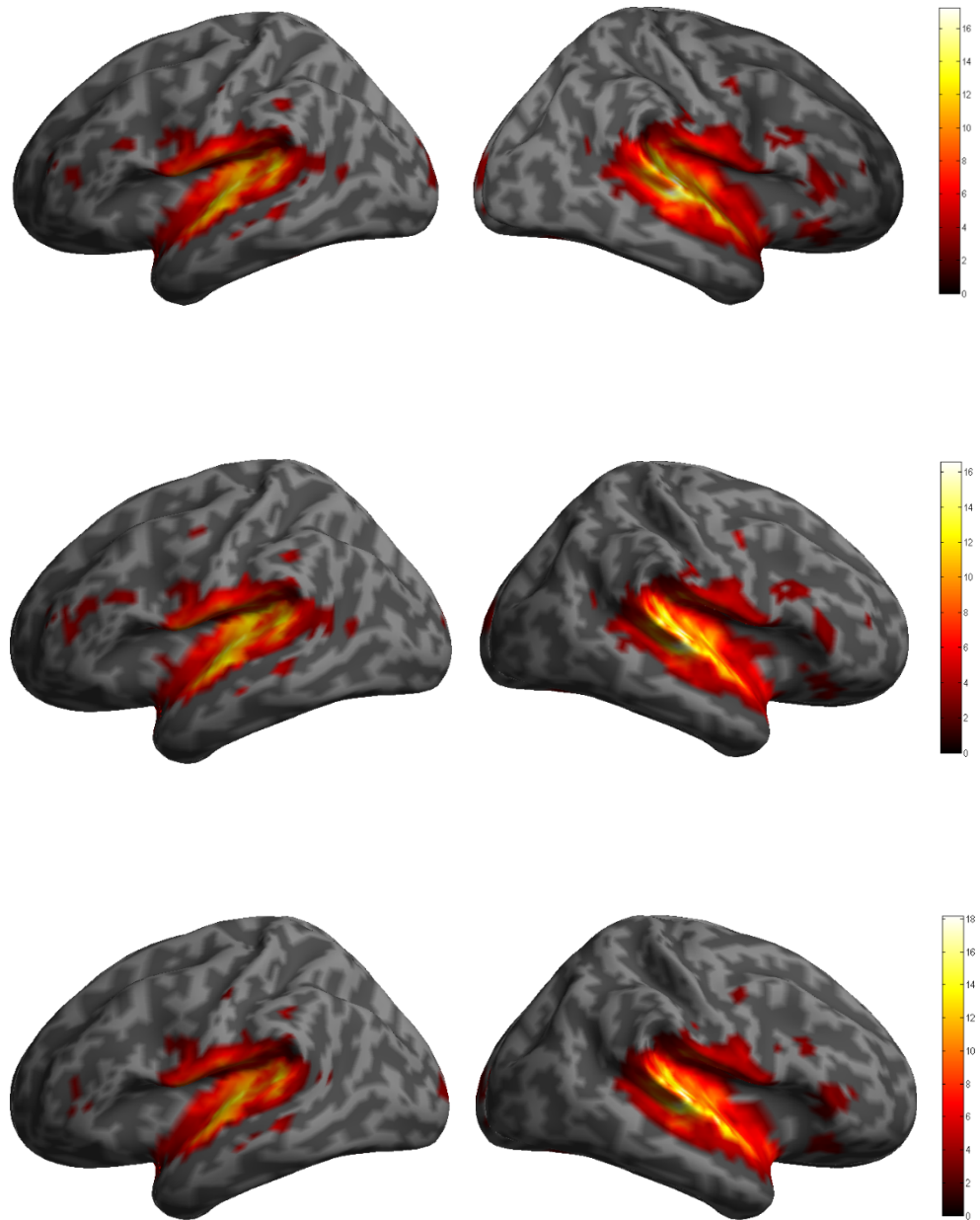


ratings of authenticity. Individual performances were calculated as Cohen's *d* scores for use in analyses of the functional data.

## 6.3 Results

### 6.3.1 All auditory emotional vocalisations compared to resting baseline

In order to explore which areas were involved in the perception of emotional vocalizations, we first compared the activations which were activated in the passive listening condition to laughter and crying against silent resting scans. Areas activated more for emotional vocalizations (i.e., laughter and crying) than for resting baseline included bilateral superior temporal gyri (STG), right superior temporal sulcus (STS), left middle frontal gyrus (MFG), left inferior frontal gyrus (IFG), bilateral precentral gyri, right cuneus, bilateral putamen, and left postcentral gyrus. In the contrast of listening all laughter against silent rest showed activation in the bilateral STG, right STS, left insula, bilateral MFG, bilateral IFG, left cuneus, right calcarine gyrus, right lingual gyrus, right precentral gyrus, and left postcentral gyrus. Similar areas including the bilateral STG, right STS, right putamen, bilateral IFG, bilateral insula lobe, right precentral gyrus, left precuneus, left cerebellum, and left postcentral gyrus, were activated in the contrast of listening crying against silent rest. (Fig. 6.1; Table 6.1)



*Figure 6.1 Activations of perceiving laughter and crying.*

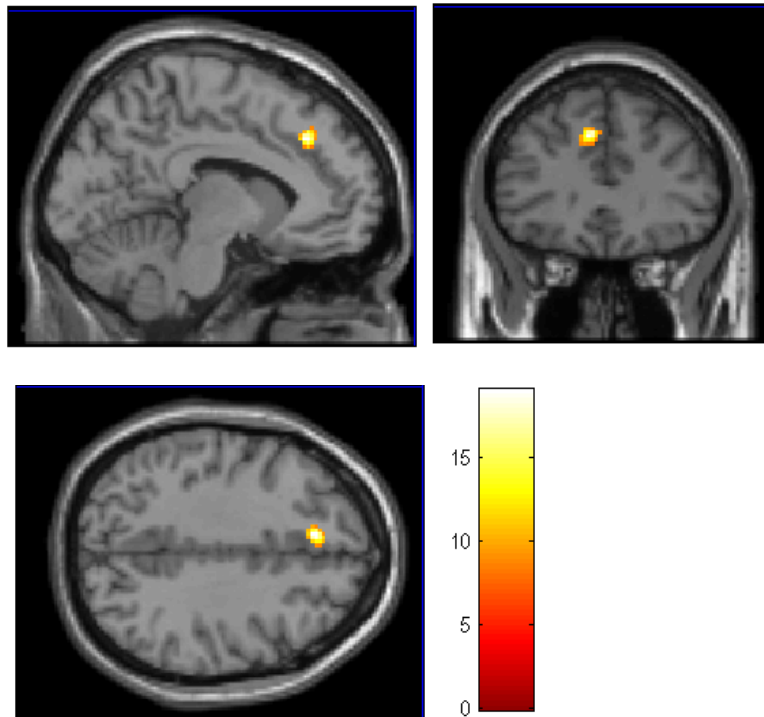
(above) Activations of perceiving laughter and crying vocalisations against resting baseline; (middle) activations of perceiving laughter against resting baseline; (below) activations of perceiving crying against resting baseline.

Table 6.1 Brain regions showing significant activation to the perception of laughter and crying against resting baseline.

Contrast	No. of voxels	Region	x	y	z	T	Z
Laughter and crying over rest	32143	R superior temporal gyrus	56	-22	4	18.62	65535
	599	L middle frontal gyrus	-38	56	20	4.93	4.03
	245	R precentral gyrus	56	-2	46	5.24	4.21
	99	L postcentral gyrus	-50	-10	50	4.05	3.48
	163	R cuneus	10	-86	42	4.04	3.48
	159	L precentral gyrus	-44	20	20	4.03	3.47
	103	R putamen	24	10	8	3.84	3.34
	72	L putamen	-20	14	2	3.75	3.28
Laughter over rest	17801	R superior temporal gyrus	56	-22	4	18.32	65535
	9050	L superior temporal gyrus	-48	-16	2	14.79	7.29
	912	L middle frontal gyrus	-14	32	2	5.66	4.44
	193	R precentral gyrus	54	-2	46	5.31	4.24
	893	L cuneus	2	-98	14	4.41	3.72
		R calcarine gyrus	18	-76	6	4.01	3.46
	95	L precentral gyrus	-52	-8	50	4.26	3.62
	259	R inferior frontal gyrus (BA 44)	46	16	24	4.19	3.58
	434	R inferior frontal gyrus (BA 45)	56	30	4	4.13	3.54
	Crying over rest	10935	R superior temporal gyrus	64	-20	6	18.94
8133		L superior temporal gyrus	-50	-22	6	15.48	7.42
9985		R thalamus	12	-30	-2	10.15	6.20
		L cerebellum	-26	-58	-26	7.31	5.20
221		R precentral gyrus	56	-2	46	4.57	3.81
136		R inferior frontal gyrus	44	16	22	4.09	3.51
303		L putamen	-20	14	2	3.53	3.12
106		L precuneus	0	-76	54	2.96	2.69
70		L postcentral gyrus	-50	-12	50	3.73	3.26
69		R putamen	24	16	6	3.67	3.22

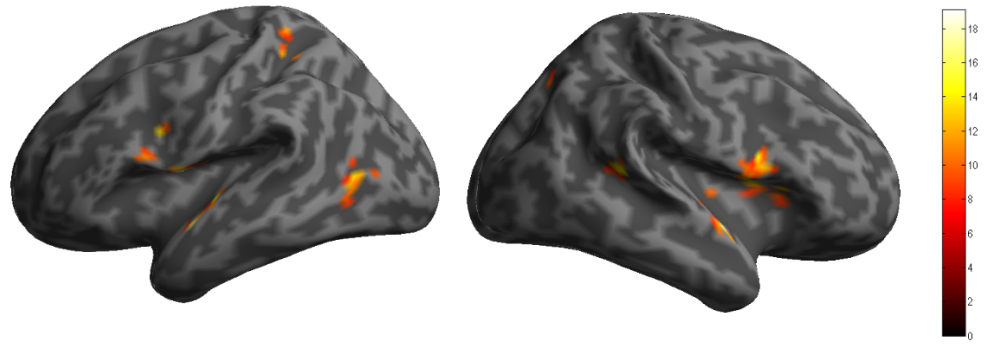
### 6.3.2 Flexible Factorial Analysis

The flexible factorial analysis allowed examination of main-effects and interactions, with factors of involuntariness (involuntary and voluntary) and expressions (laughter and crying). We found that the left superior frontal gyrus (SFG; BA 8) showed more activation in the main effect of expressions (Fig. 6.2; Table 6.2). No region was found to be more activated in the main effect of authenticity. The left STG, right precuneus, right temporal pole, right insula, bilateral middle temporal gyrus (MTG), left IFG, left middle occipital gyrus, right lingual gyrus, left MFG, and left postcentral gyrus were more activated in the interaction between involuntariness and expressions (Fig. 6.3; Table 6.2).



*Figure 6.2 Main effect of perceiving expressions*

Left superior frontal gyrus showed more activation in the main effect of expressions, shown at  $x = -8, y = 32, z = 38$ .



*Figure 6.3 Interaction of flexible factorial design*

Left STG, right precuneus, right temporal pole, right insula, bilateral middle temporal gyrus (MTG), left IFG, left middle occipital gyrus, right lingual gyrus, left MFG, and left postcentral gyrus were identified in the interaction between involuntariness and expressions.

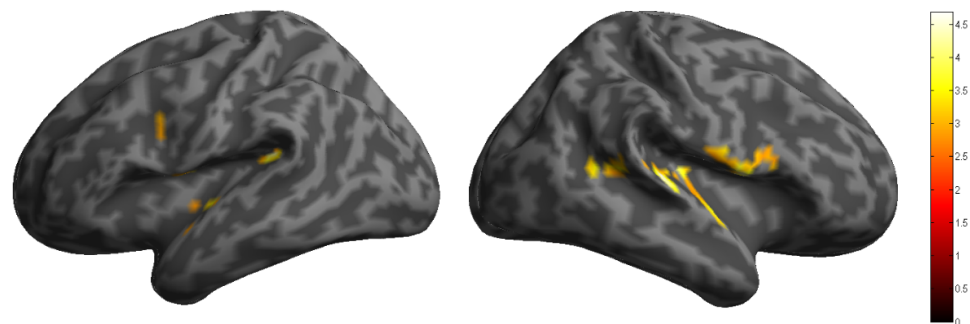
Table 6.2 Regions showed significant activities in the flexible factorial analysis

Contrast	No. of voxels	Region	x	y	z	F	Z
Main effect of expression	89	Left superior frontal gyrus	-8	32	38	19.06	3.99
Interaction	774	L superior temporal gyrus	-54	-2	-2	24.26	4.48
	742	R temporal pole	54	4	-4	19.17	4.00
	197	L middle occipital gyrus	-50	-78	16	14.12	3.43
	190	R precuneus	16	-60	40	20.33	4.12
	143	R lingual gyrus	14	-72	-4	13.80	3.39
	97	L middle frontal gyrus	-32	56	26	11.96	3.15
	90	L precentral gyrus	-24	-38	58	11.78	3.12
	86	R middle temporal gyrus	50	-44	12	15.92	3.65
	83	L inferior frontal gyrus	-62	8	14	14.50	3.48
	74	R pars triangularis of the inferior frontal gyrus	40	24	12	14.50	3.48

### 6.3.3 Direct comparison of involuntary and voluntary conditions in each expression

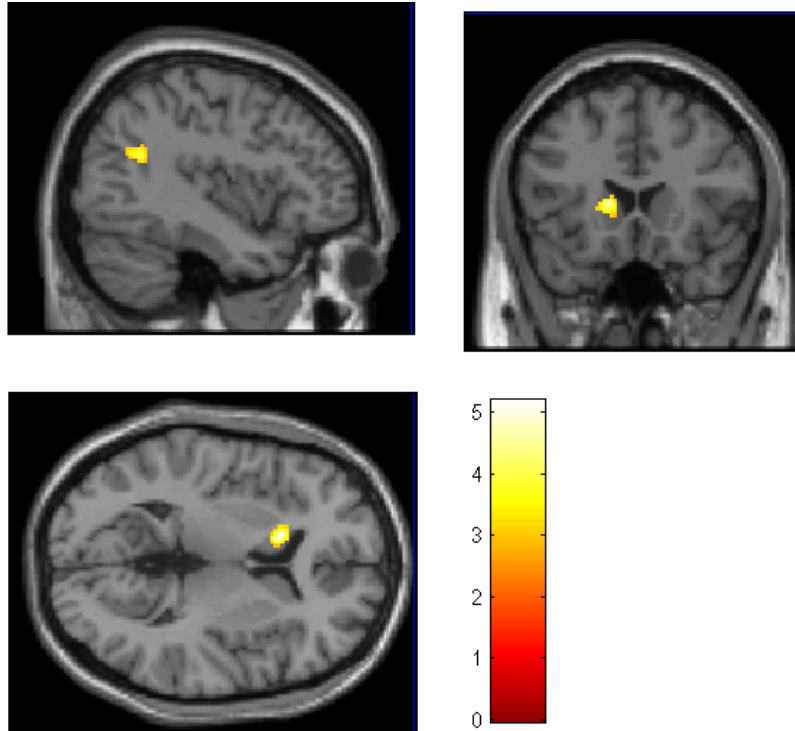
#### 6.3.3.1 The perception of laughter

In order to examine which areas were more activated during the perception of involuntary laughter (IL) compared to voluntary laughter (VL), a direct comparison between these two conditions was performed. Areas which were activated more for the perception of involuntary laughter than for voluntary laughter were the right STG, right rolandic operculum, right insula lobe, and left IFG (Fig. 6.4). Comparing the perception of voluntary laughter to involuntary laughter, the left caudate nucleus and left MTG showed more activations (Fig. 6.5).



*Figure 6.4 Activations of perceiving involuntary over voluntary laughter*

Right STG, right rolandic operculum, right insula lobe, and left IFG showed more activation for hearing involuntary laughter than for voluntary laughter.



*Figure 6.5 Activations of perceiving voluntary over involuntary laughter*

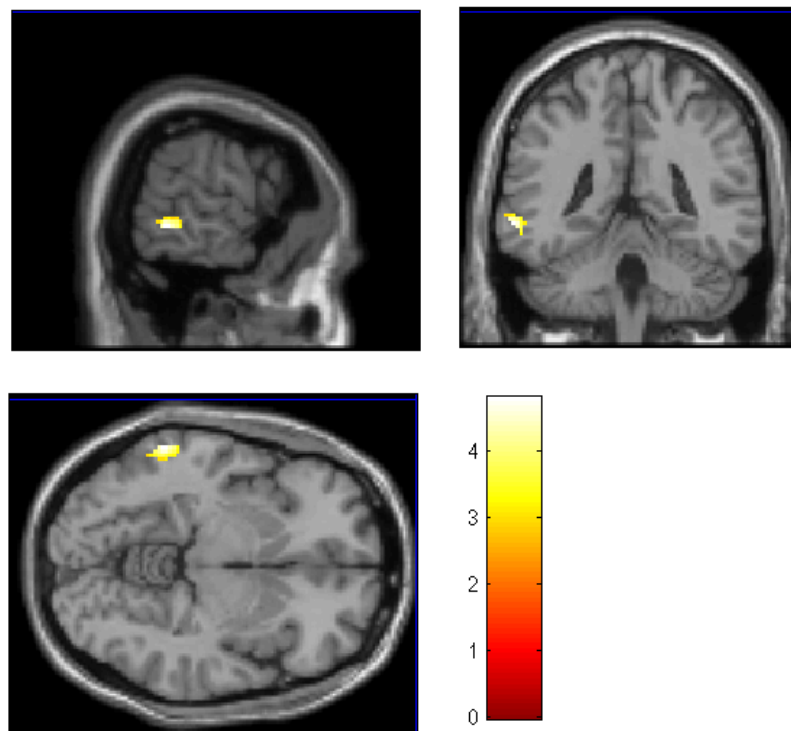
Left angular gyrus and left caudate were more activated for hearing voluntary laughter than for involuntary laughter. Shown at  $x = -40, y = 20, z = 5.6$ .

Table 6.3 Regions were identified by the contrast between involuntary laughter (IL) and voluntary laughter (VL).

Contrast	No. of voxels	Region	x	y	z	T	Z
IL > VL	1160	R superior temporal gyrus	58	-24	10	4.75	3.96
		R rolandic operculum	52	2	0	4.56	3.81
		R primary auditory cortex (BA 41)	34	-26	12	3.85	3.35
		R insula lobe	50	0	-2		
	303	L superior temporal gyrus	-50	-25	-4	5.15	4.16
		L middle temporal gyrus	-46	-20	-2	3.37	3.00
132	R fusiform gyrus	42	-50	10	4.16	3.55	
	R superior temporal gyrus	46	-42	14	3.67	3.22	
75	L inferior frontal gyrus	-36	2	24	3.18	2.87	
VL > IL	90	L caudate nucleus	-14	20	6	5.19	4.18
	80	L angular gyrus	-40	-56	24	4.14	3.54

### 6.3.3.2 The perception of crying

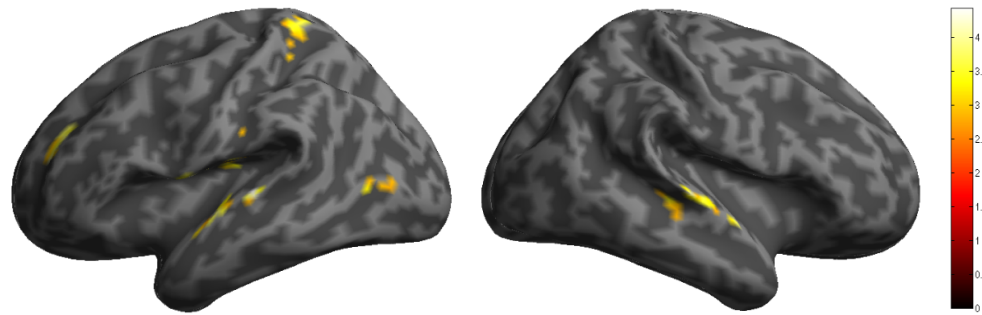
In order to examine which areas were more activated during the perception of involuntary crying (IC) compared to voluntary crying (VC), a direct comparison between these two conditions was performed. The left posterior MTG (BA 21) showed more activation for the perception of involuntary crying than for voluntary crying (Fig. 6.6, Table 6.4). However, several areas showed more activations to the reverse contrast, such as bilateral MTG, left Heschl's gyrus, right thalamus, right precentral gyrus, right temporal pole, bilateral STG, bilateral MFG, left SFG, left superior parietal lobule (SPL), left precuneus, right lingual gyrus, and left middle occipital gyrus showed more activations to voluntary crying than to involuntary crying (Fig. 6.7, Table 6.4).



*Figure 6.6 Activations of perceiving involuntary over voluntary crying*

Left posterior middle temporal gyrus showed more activation to the perception of involuntary crying than to voluntary crying. Shown at  $x = -62, y = -42, z = -6$ .





*Figure 6.7 Activations of perceiving voluntary over involuntary crying*

Bilateral MTG, left Heschl's gyrus, right thalamus, right precentral gyrus, right temporal pole, bilateral STG, bilateral MFG, left SFG, left superior parietal lobule (SPL), left precuneus, right lingual gyrus, and left middle occipital gyrus showed more activations to voluntary crying than to involuntary crying.

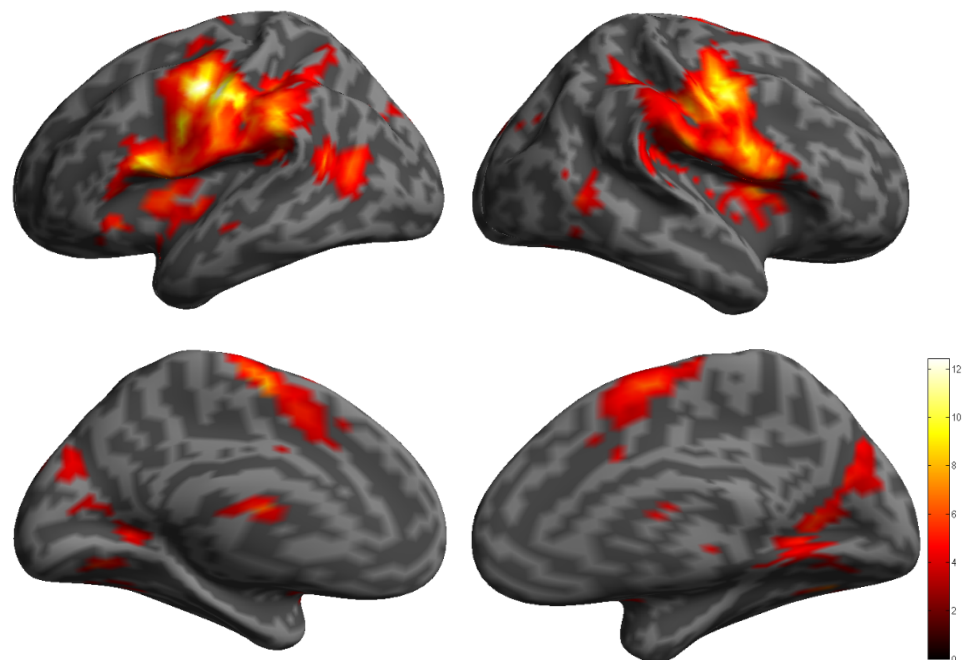
Table 6.4 Regions identified by the contrast between involuntary crying and voluntary crying.

Contrast	No. of voxels	Region	x	y	z	T	Z
IC > VC	86	L middle temporal gyrus	-62	-42	-6	4.81	3.96
VC > IC	734	L middle temporal gyrus	-66	-22	2	6.41	4.81
		L Heschls gyrus	-48	-12	8	6.18	4.70
	122	R Thalamus	22	-22	20	4.65	3.86
	166	R precentral	58	4	44	4.62	3.85
		R middle frontal gyrus	50	-2	52	3.42	3.04
	397	R temporal pole	64	4	-2	4.36	3.68
		R superior frontal gyrus	66	-18	0	4.35	3.68
	238	L middle frontal gyrus	-20	38	24	4.22	3.60
		L superior frontal gyrus	-30	56	24	3.72	3.26
	181	L superior parietal lobule	-24	-34	50	4.01	3.46
		L precuneus	-16	-48	54	3.66	3.22
	84	R middle temporal gyrus	48	-32	0	3.93	3.40
	76	R lingual gyrus	20	-66	0	3.72	3.26
	69	L middle occipital gyrus	-50	-80	14	3.65	3.21

### 6.3.4 Localizers

#### 6.3.4.1 Orofacial movement localizer (motor task)

Participants were instructed in the motor task to move their facial muscles to mimic happy and frowning facial expressions. An orofacial movement localizer then identified brain regions which were more activated during this orofacial movements task against rest. These areas were activated along the upper bank of bilateral temporal gyrus including STG and MTG, and also in the sensorimotor areas such as the right precentral gyrus and left postcentral gyrus extended to the left precuneus, and bilateral cerebellum (Fig. 6.8, Table 6.5). This motor network was then saved as a binary motor mask to later illustrate the overlap between perceptual responses to emotional vocalisations and brain regions supporting orofacial movements.



*Figure 6.8 Regions identified by orofacial movement localizer.*

Table 6.5 Regions identified by orofacial movement localizer. S, smile; F, frown.

Contrast	No. of voxels	Region	x	y	z	T	Z
S + F > Rest	5206	L cerebellum	-18	-62	-18	15.64	7.45
		R cerebellum	16	-62	-18	11.48	6.56
	26967	L postcentral gyrus	-44	-12	42	12.67	6.85
		R precentral gyrus	56	-8	42	10.62	6.33
	927	L middle temporal gyrus	-58	-64	14	8.28	5.58
	378	R middle temporal gyrus	56	-62	0	5.68	4.45
	169	L precuneus	-24	-54	4	4.98	4.06

#### 6.3.4.2 Theory of mind localizers (TOM task)

In the theory of mind task, participants answered True or False to the stories which were either described with false belief (BELIEF) or with false photographs and maps (PHOTO). The regions which showed more activations to stories in the BELIEF condition than to stories in the PHOTO condition were identified as theory of mind localizers. The bilateral angular gyri, bilateral MTG, bilateral precuneus, right MFG, left superior frontal gyrus (SFG), left superior medial gyrus, bilateral cerebellum, left inferior occipital gyrus, bilateral IFG, left anterior cingulate cortex (ACC), and right posterior cingulate cortex (PCC) showed more activations in the BELIEF condition than in the PHOTO condition (Fig. 6.9, Table 6.6). This theory of mind network was then saved as a binary mask (TOM mask) to later illustrate the overlap between perceptual responses to emotional vocalisations and brain regions supporting the mentalising network.

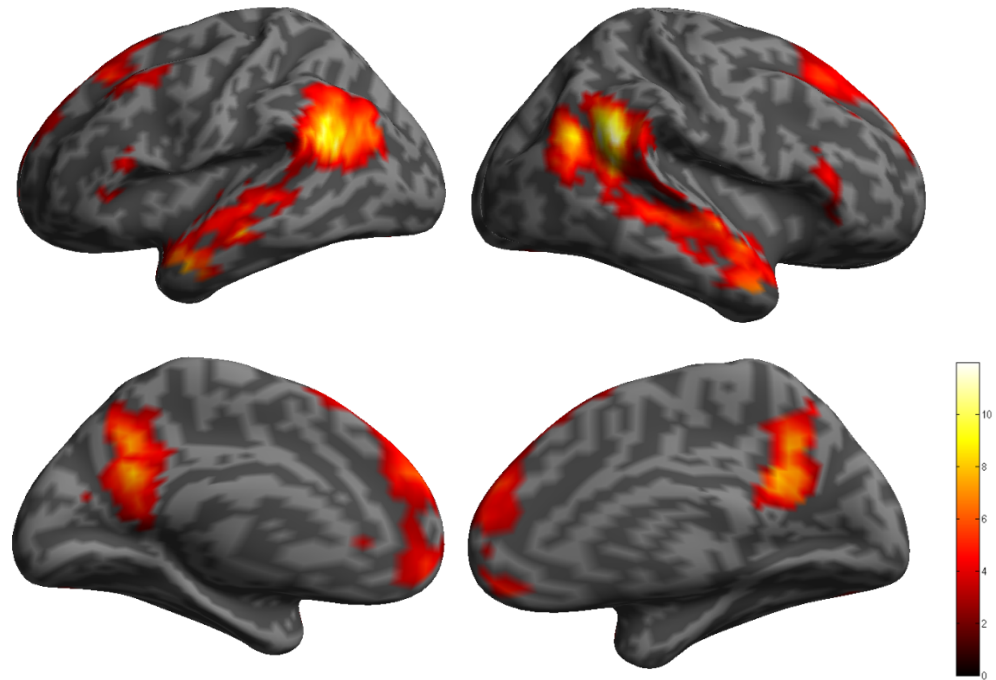


Figure 6.9 Theory of mind network.

Brain regions showed more activations in the false belief condition than in the photo condition.

Table 6.6 Regions identified in the theory of mind network.

Contrast	No. of voxels	Region	x	y	z	T	Z
Belief > Photo	6504	R angular gyrus	52	-52	24	12.27	6.48
		R middle temporal gyrus	64	-4	-14	8.97	5.62
	5559	L angular gyrus	-48	-54	28	11.34	6.27
		L middle temporal gyrus	-46	-54	20	10.51	6.06
	2870	L precuneus	-8	-54	34	8.71	5.54
		R posterior cingulate cortex	6	-50	28	7.93	5.28
		R precuneus	6	-54	36	7.84	5.24
	7956	R middle frontal gyrus	24	28	38	7.64	5.17
		L superior frontal gyrus	-10	54	40	7.36	5.06
		L superior medial gyrus	-10	50	24	7.30	5.04
	917	L cerebellum	-28	-82	-28	5.63	4.31
		L inferior occipital gyrus	-28	-82	-12	3.09	2.76
	356	R inferior frontal gyrus	58	28	12	5.16	4.07
	87	L inferior frontal gyrus	-54	22	16	4.77	3.86
	637	R cerebellum	28	-82	-30	4.38	3.62
	116	L anterior cingulate cortex	-4	28	-6	4.14	3.48

### 6.3.5 Common areas for listening to emotional vocalisations and the motor task

The contrast of hearing all emotional vocalisations (i.e., laughter and crying) against silent rest was masked inclusively by activations during the orofacial movement task. Regions which showed activations in both tasks were the bilateral STG, bilateral cerebellum, right insula lobe, right rolandic operculum, left thalamus, bilateral caudate nucleus, right precentral gyrus, right IFG, left postcentral gyrus, and left MTG (Fig. 6.10, Table 6.7).

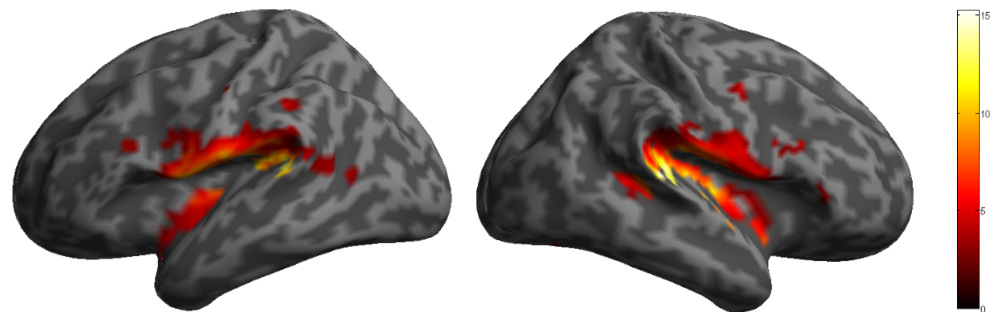
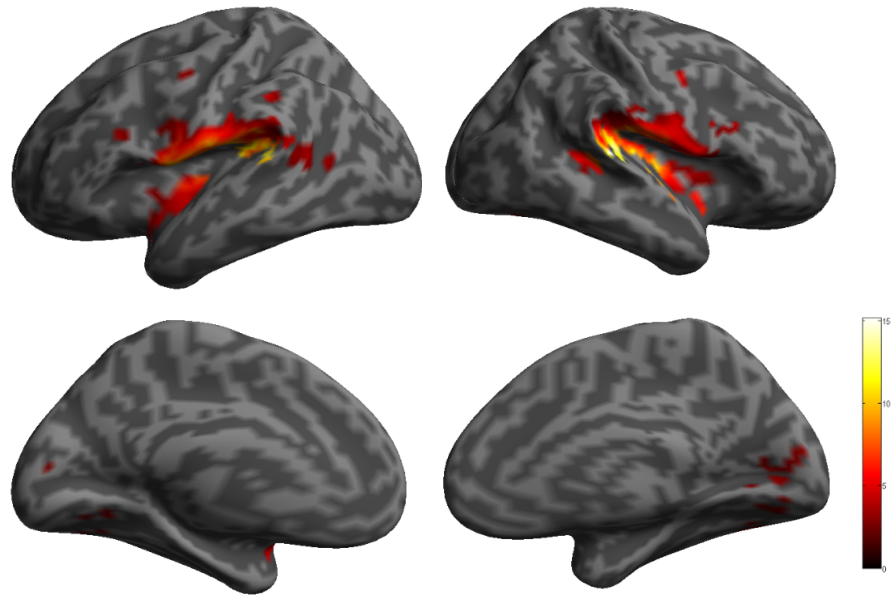


Figure 6.10 Common brain regions identified by listening to emotional vocalisations (i.e., laughter and crying) and the motor task.

Table 6.7 Brain regions showing significant activation during the perception of all vocalizations over rest, inclusively masked with the motor task.

Contrast	No. of voxels	Region	x	y	z	T	Z
Laughter + crying > rest with motor mask	4553	R superior temporal gyrus	66	-20	8	16.38	7.57
	4067	L superior temporal gyrus	-62	-36	18	13.35	7.00
		L Heschl's Gyrus	-48	-12	4	12.87	6.89
	4972	R cerebellum	26	-60	-24	8.27	5.58
		L cerebellum	-28	-58	-24	8.25	5.57
	244	R precentral gyrus	56	-2	46	5.23	4.21
	144	R inferior frontal gyrus	46	16	22	4.45	3.74
	99	L postcentral gyrus	-50	-10	50	4.05	3.48
	108	L inferior frontal gyrus	-44	20	20	4.03	3.47
		L precentral gyrus	-54	12	36	3.03	2.75

The contrast of hearing all laughter conditions over silent rest was masked inclusively by activations during the motor task, showed common activations of the bilateral STG, left rolandic operculum, left Heschl's gyrus, bilateral cerebellum, bilateral precentral gyrus, bilateral thalamus, left caudate nucleus, bilateral IFG, and right calcarine gyrus (Fig. 6.11, Table 6.8).



*Figure 6.11 Common brain regions identified by the contrast of hearing laughter against rest and the motor task over rest.*

Table 6.8 Brain regions showing significant activation during the contrast of hearing laughter over rest, inclusively masked with the contrast of motor task over rest.

Contrast	No. of voxels	Region	x	y	z	T	Z
Laughter > rest with motor mask	4082	R superior temporal gyrus	66	-28	10	15.98	7.51
	4215	L superior temporal gyrus	-62	-36	18	13.55	7.04
		L rolandic operculum	-36	-32	14	12.55	6.82
		L Heschl's Gyrus	-48	-12	4	12.05	6.70
	3602	L cerebellum	-28	-58	-24	7.69	5.36
		R cerebellum	26	-60	-24	7.49	5.28
	193	R precentral gyrus	54	-2	46	5.31	4.24
	116	R thalamus	12	-22	10	3.92	3.40
		R caudate nucleus	18	-6	24	3.90	3.38
	144	R inferior frontal gyrus	46	16	24	4.19	3.58
	102	L caudate nucleus	-18	-6	24	4.08	3.50
		L thalamus	-10	-12	14	3.98	3.43
	132	L inferior frontal gyrus	-42	20	20	4.06	3.49
		L precentral gyrus	-50	10	30	3.28	2.94
	204	R calcarine gyrus	18	-76	6	4.01	3.46

The contrast of hearing crying over silent rest was masked inclusively by activations during the motor task, showing common activation of the bilateral STG, left Heschl's gyrus, bilateral cerebellum, right precentral gyrus, left postcentral gyrus, left thalamus, and right IFG (Fig. 6.12, Table 6.9).

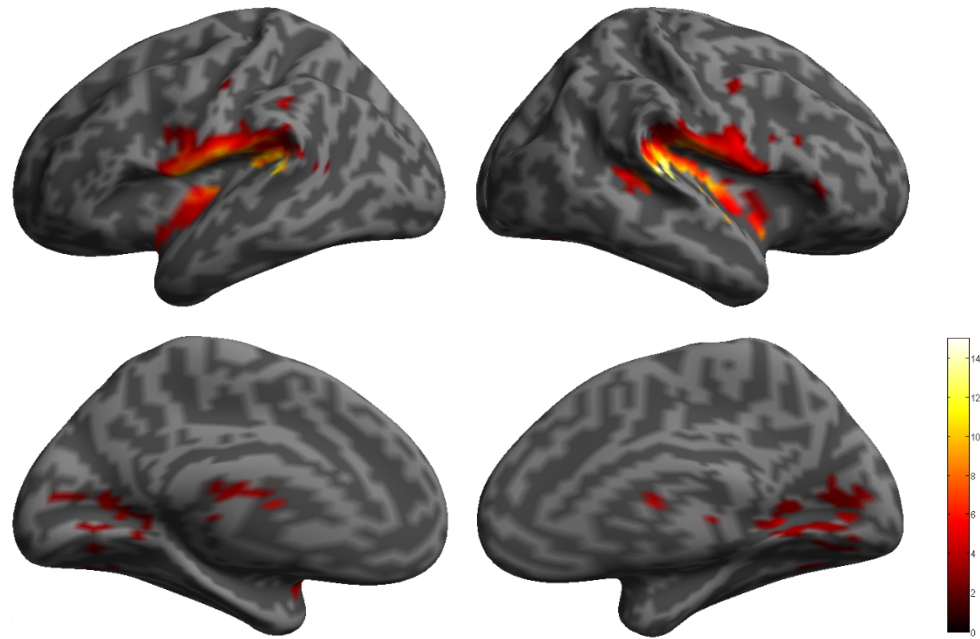


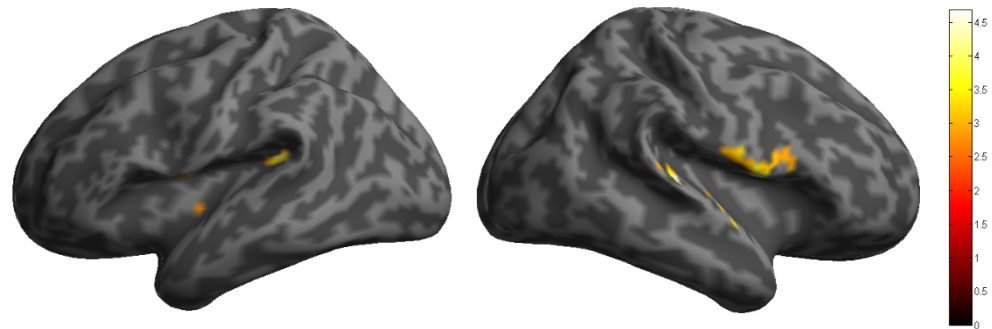
Figure 6.12 Common brain regions identified by the contrast of hearing crying against rest and the motor task.

Table 6.9 Brain regions showing significant activation during the contrast of hearing crying over rest, inclusively masked with the contrast of motor task over rest.

Contrast	No. of voxels	Region	x	y	z	T	Z
Crying > rest with motor mask	3967	R superior temporal gyrus	66	-20	8	17.48	7.75
	3511	L superior temporal gyrus	-58	-34	14	13.77	7.09
		L Heschl's Gyrus	-48	-12	4	13.32	6.99
	4578	L cerebellum	-26	-58	-26	7.31	5.20
		R cerebellum	28	-60	-22	6.57	4.88
	494	L thalamus	-14	-12	16	5.04	4.09
	220	R precentral gyrus	56	-2	46	4.57	3.81
	68	R inferior frontal gyrus	44	16	22	4.09	3.51
	70	L postcentral gyrus	-50	-12	50	3.73	3.26

The direct contrast of hearing involuntary laughter against voluntary laughter was masked inclusively by activations during the motor task, showing common activations of the bilateral STG and right rolandic operculum. No common activation was found for inverse comparison (i.e., voluntary over involuntary laughter) and the orofacial movement task (Fig. 6.13, Table 6.10).



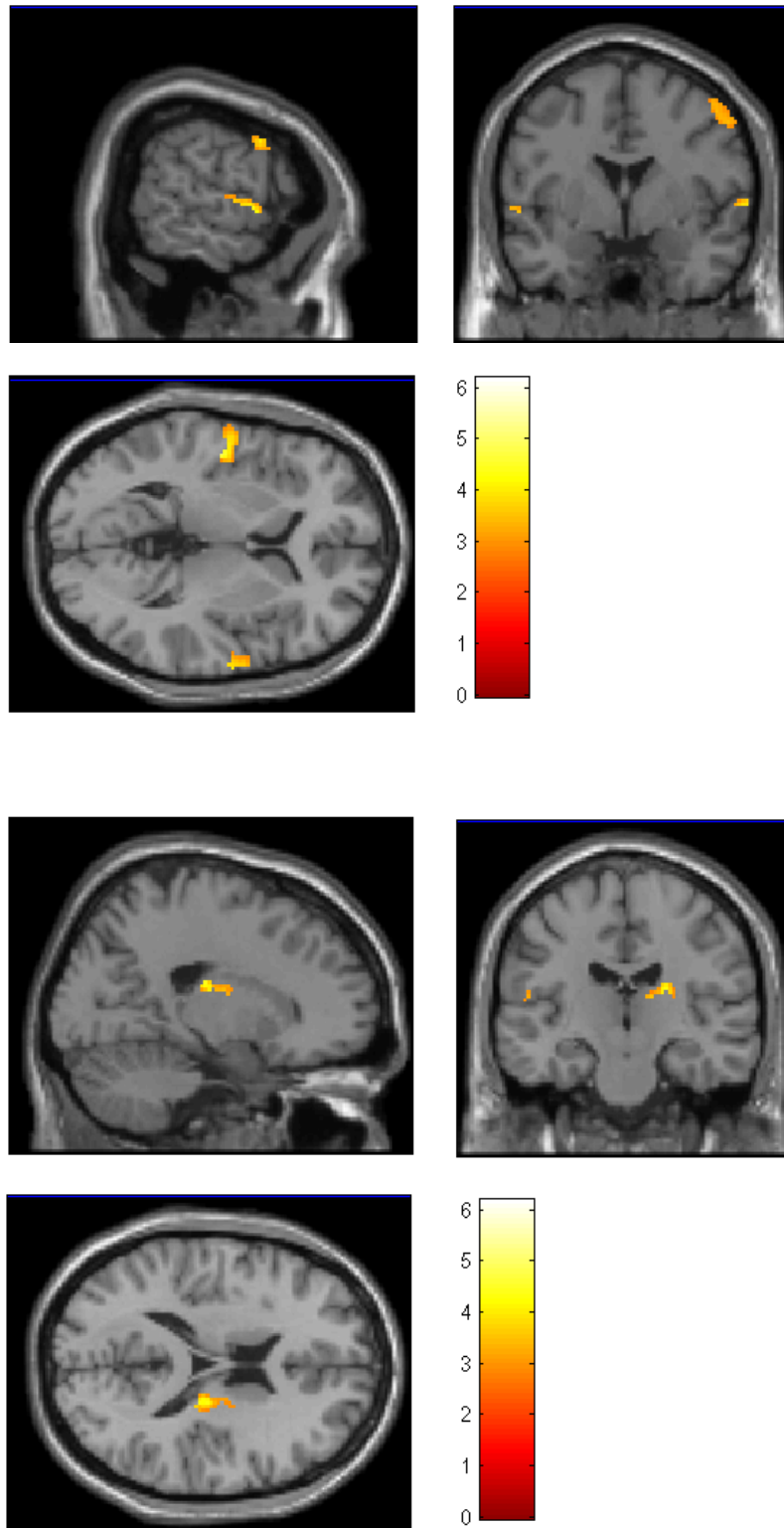


*Figure 6.13 Common brain regions identified by the contrast of hearing involuntary laughter against voluntary laughter and the motor task over rest.*

Table 6.10 Brain regions showing significant activation during the contrast of hearing involuntary over voluntary laughter, inclusively masked with the contrast of motor task over rest.

Contrast	No. of voxels	Region	x	y	z	T	Z
IL > VL with motor mask	163	L superior temporal gyrus	-50	-2	-4	5.15	4.16
	90	L superior temporal gyrus	-42	-40	14	4.82	3.97
	803	R superior temporal gyrus	58	-24	10	4.75	3.93
		R rolandic operculum	52	2	0	4.56	3.81

The direct contrast of hearing involuntary crying over voluntary crying showed no common activations inclusively with activations during the motor mask. However, the reverse contrast showed common activations of the left Heschl's gyrus, left STG, right precentral gyrus, right MFG, and right thalamus when inclusively masked by the activation of orofacial movements task over rest (Fig. 6.14, Table 6.11).



*Figure 6.14 Common areas for the contrast of hearing voluntary crying against involuntary crying and the motor mask*

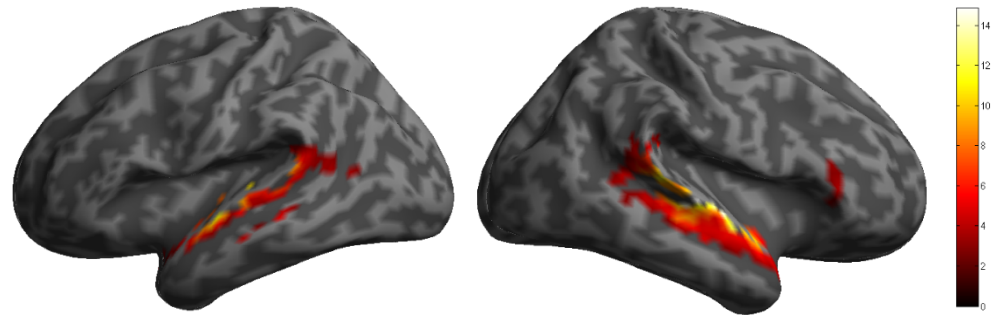
(upper, shown at  $x = 62, y = 0, z = 4$ ; lower, shown at  $x = 22, y = -18, z = 20$ ).

Table 6.11 Brain regions showing significant activation during the contrast of hearing voluntary over involuntary crying, inclusively masked with the contrast of motor task over rest.

Contrast	No. of voxels	Region	x	y	z	T	Z
VC > IC with motor mask	161	L Heschl's gyrus	-48	-12	8	6.18	4.70
		L superior temporal gyrus	-58	-6	2	4.30	3.64
		R thalamus	14	-18	14	3.46	3.07
	156	R precentral gyrus	58	4	44	4.62	3.85
		R middle frontal gyrus	50	-2	52	3.42	3.04
	93	R temporal pole	64	4	0	4.26	3.62
		R superior temporal gyrus	66	-2	2	4.00	3.45

### 6.3.6 Common areas for listening to emotional vocalizations and the TOM task

The contrast of hearing all emotional vocalisation conditions (i.e., laughter and crying) against rest was masked inclusively by activations during the TOM task (BELIEF > PHOTO). Regions which showed activations in both contrasts were the bilateral STG, right superior temporal sulcus (STS), bilateral MTG, bilateral cerebellum, and right IFG (Fig. 6.15, Table 6.12).



*Figure 6.15 Common areas for listening to laughter and crying and for theory of mind task.*

Table 6.12 Brain regions showing significant activation during the contrast of hearing laughter and crying over rest, inclusively masked by the theory of mind task.

Contrast	No. of voxels	Region	x	y	z	T	Z
Laughter + crying > rest with TOM mask	2683	R superior temporal gyrus	54	-20	0	15.64	7.45
		R temporal pole	56	6	-10	11.71	6.62
	1590	L middle temporal gyrus	-60	-12	-2	12.39	6.78
		L superior temporal gyrus	-46	-24	2	12.25	6.75
	512	L cerebellum	-14	-78	-38	5.86	4.54
	225	R cerebellum	18	-74	-22	4.85	3.99
	169	R inferior frontal gyrus	52	30	4	4.49	3.77

The contrast of hearing laughter against rest was masked inclusively by activations during the TOM task. Regions which showed activations in both contrasts were the bilateral STG, right STS, left MTG, and bilateral cerebellum (Fig. 6.16, Table 6.13).

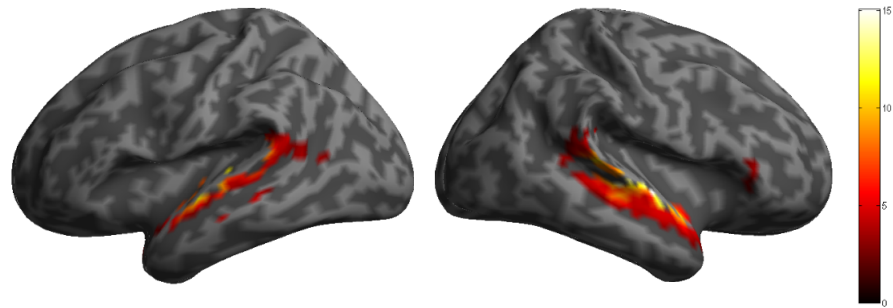
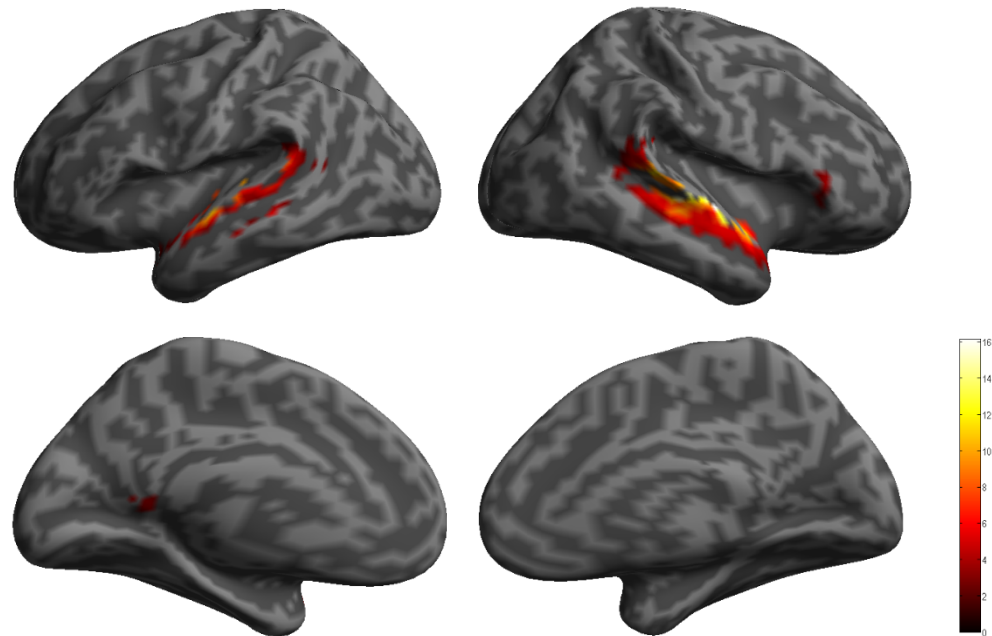


Figure 6.16 Common areas for the contrast of hearing laughter against rest and the TOM task.

Table 6.13 Brain regions showing significant activation during the contrast of hearing laughter over rest, inclusively masked by the TOM task.

Contrast	No. of voxels	Region	x	y	z	T	Z
Laughter > rest with TOM mask	2621	R superior temporal gyrus	62	-14	0	15.29	7.38
	1593	L middle temporal gyrus	-60	-12	-2	12.56	6.82
		L superior temporal gyrus	-46	-24	2	11.79	6.64
	487	L cerebellum	-12	-80	-40	6.32	4.77
	82	R cerebellum	16	-80	-38	4.95	4.04
	91	R cerebellum	18	-76	-20	4.23	3.60
	190	R inferior frontal gyrus	56	30	4	4.13	3.54

The contrast of hearing crying against rest was masked inclusively by activations during the TOM task. Regions which showed activations in both tasks were the bilateral STG, right STS, left MTG, right temporal pole, bilateral cerebellum, left calcarine gyrus, and right IFG (Fig. 6.17, Table 6.14).

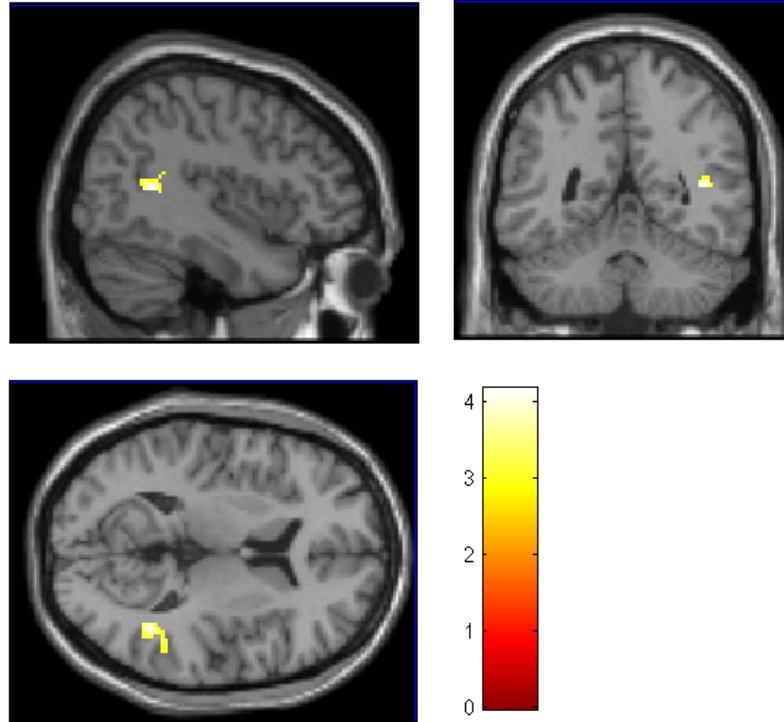


*Figure 6.17 Common areas for the contrast of hearing crying over rest and the TOM task.*

Table 6.14 Brain regions showing significant activation during the contrast of hearing crying against rest, inclusively masked by the contrast of TOM task.

Contrast	No. of voxels	Region	x	y	z	T	Z
Crying > rest with TOM mask	2538	R superior temporal gyrus	58	-6	-4	16.12	7.53
		R temporal pole	54	6	-12	11.94	6.68
	1396	L superior temporal gyrus	-46	-24	2	12.25	6.75
		L middle temporal gyrus	-60	-14	0	11.52	6.57
	393	L cerebellum	-16	-78	-36	5.39	4.29
	70	L calcarine gyrus	-6	-52	6	4.64	3.86
	126	R inferior frontal gyrus	48	30	2	4.62	3.85
	165	R cerebellum	24	-72	-38	4.37	3.69

The contrast of hearing involuntary laughter over voluntary laughter, masked inclusively with the TOM network, revealed common activation of the right STS (Fig. 6.18, Table 6.15).



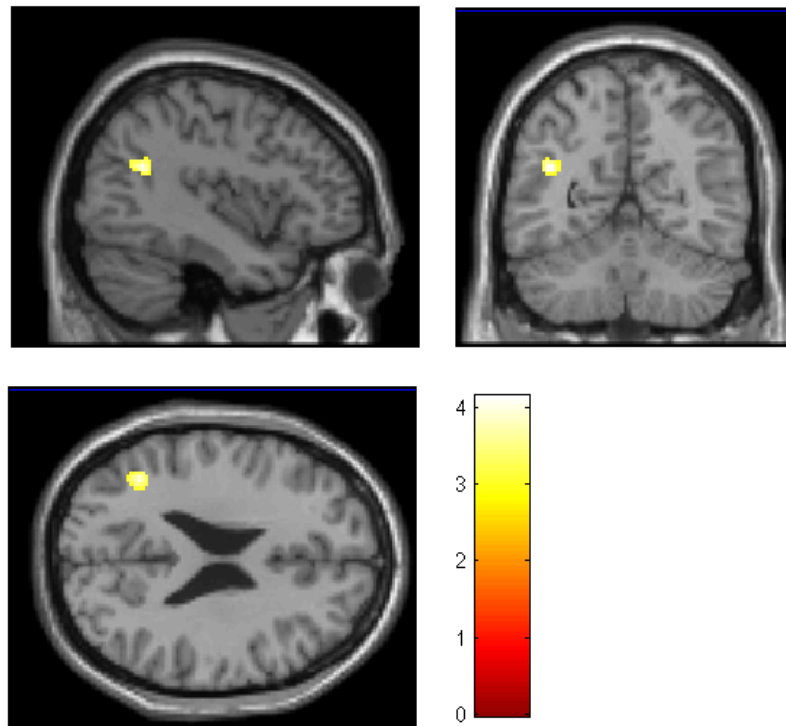
*Figure 6.18 Common areas for the contrast of hearing involuntary laughter against voluntary laughter and the TOM task*

(shown at  $x = 46, y = -42, z = 14$ ).

Table 6.15 Brain regions showing significant activation during the contrast of hearing involuntary over voluntary laughter, inclusively masked by the contrast of TOM task.

Contrast	No. of voxels	Region	x	y	z	T	Z
IL > VL with TOM mask	107	R superior temporal sulcus	46	-42	14	3.68	3.23

The contrast of hearing voluntary over involuntary laughter, masked with the TOM network, revealed that the left angular gyrus showed significant activation in the contrast of hearing voluntary over involuntary laughter and during the TOM task (Fig. 6.19, Table 6.16).



*Figure 6.19 Common areas for the contrast of hearing voluntary laughter against involuntary laughter and the TOM task*

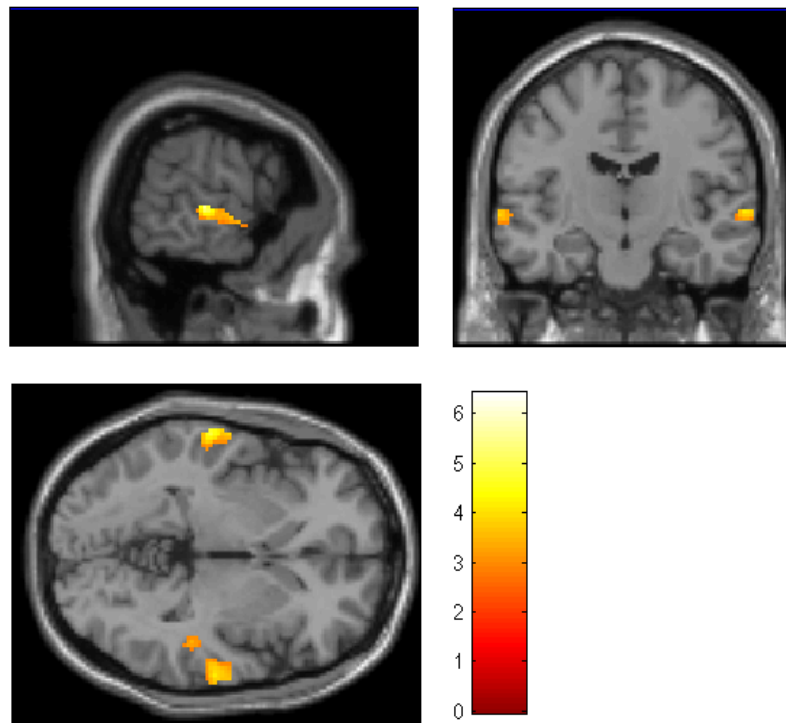
(shown at  $x = -40, y = -56, z = 24$ )

Table 6.16 Brain regions showing significant activations during the contrast of hearing voluntary laughter over involuntary laughter, inclusively masked by the contrast of TOM task.

Contrast	No. of voxels	Region	x	y	z	T	Z
VL > IL with TOM mask	79	L angular gyrus	-40	-56	24	4.14	3.54



The contrast of hearing voluntary over involuntary crying, masked inclusively with the TOM network, revealed that the bilateral MTG and bilateral STG showed significant activation in the contrast of hearing voluntary over involuntary crying and during the TOM task (Fig. 6.20, Table 6.17). Nothing significant was shown in the opposite contrast.



*Figure 6.20 Common areas for the contrast of hearing voluntary crying against involuntary crying and the TOM task*

(shown at  $x = -62, y = -18, z = 0$ )

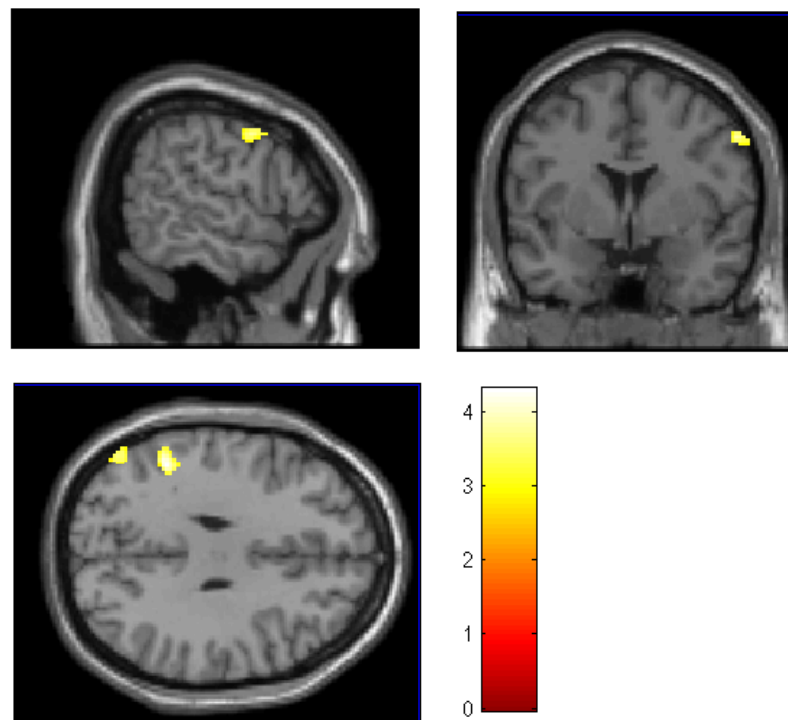
Table 6.17 Brain regions showed significant activations during the contrast of hearing voluntary crying over involuntary crying, inclusively masked by the TOM task.

Contrast	No. of voxels	Region	x	y	z	T	Z
VC > IC with TOM mask	126	L middle temporal gyrus	-66	-22	2	6.41	4.81
		L superior temporal gyrus	-62	-4	-6	3.39	3.02
	116	R superior temporal gyrus	66	-18	0	4.35	3.68
		81	R middle temporal gyrus	48	-32	0	3.93

### 6.3.7 Individual differences of the perception of laughter and crying

#### 6.3.7.1 Authenticity ratings on laughter and crying

The regression analysis on the contrast Laughter>rest identified activations in the left supramarginal gyrus, left angular gyrus, left MTG, and right precentral gyrus which were positively correlated with behavioural performance on authenticity ratings on laughter. Among these areas, the left supramarginal gyrus and the left MTG were both activated by the motor task and by the theory of mind task. However, the right precentral gyrus showing positive correlation between the perception of laughter and individual performance was only activated by the motor task, and the left angular gyrus was only activated by the theory of mind task. There was no region in which activation was found to be negatively correlated with cerebral activity to laughter and the individual performance on the authenticity ratings on laughter (Fig. 6.21, Table 6.18).



*Figure 6.21 Brain activations identified in the contrast of hearing laughter against rest positively correlated with the performance on the authenticity ratings on laughter*

(shown at  $x = 60, y = -2, z = 30$ ).

Table 6.18 Brain regions showing significant positive correlation between performance on the authenticity rating task on laughter and the activations during the contrast of hearing laughter against silent rest.

Contrast	No. of voxels	Region	x	y	z	T	Z
All laughs > rest (+)	301	L supramarginal gyrus	-46	-44	30	4.30	3.62
		L middle temporal gyrus	-52	-48	22	4.05	3.46
	87	L angular gyrus	-50	-72	34	3.81	3.30
	70	R precentral gyrus	58	2	42	3.75	3.26

The regression analysis on the contrast Crying>rest identified activations in the left IFG, right temporal pole, and right insula lobe which were positively correlated with behavioural performance on authenticity ratings on crying. Among these areas, the left IFG was both identified in the motor task and the TOM task, and the right insula lobe and the right IFG were only identified in the TOM task (Fig. 6.22, Table 6.19).

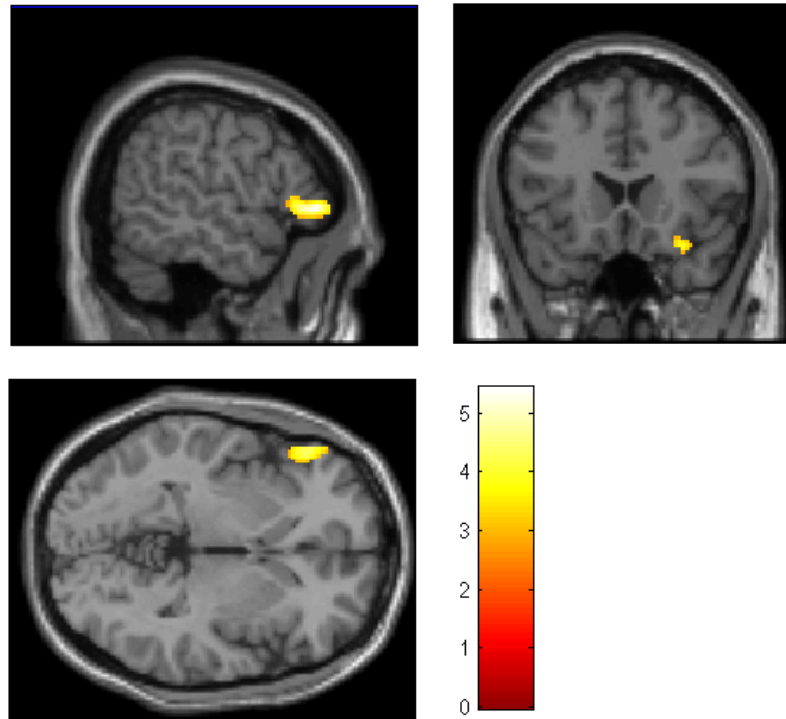


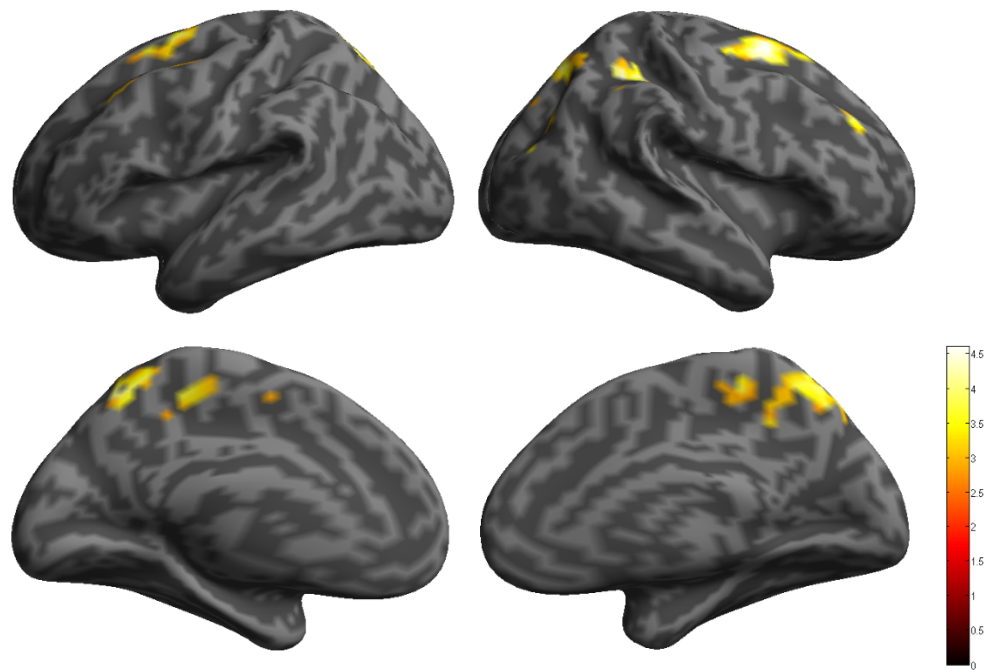
Figure 6.22 Brain activations identified in the contrast of hearing crying against rest positively correlated with the performance on the authenticity ratings on crying

(shown at  $x = -51, y = 20, z = 2$ ).

Table 6.19 Brain regions showed significant positive correlation between the performance on authenticity ratings on crying and the activations during the contrast of hearing crying against silent rest, with inclusively masked by motor and TOM task.

Contrast	No. of voxels	Region	x	y	z	T	Z
All cries > rest (+)	221	L inferior frontal gyrus	-54	38	2	5.42	4.28
	68	R temporal pole	34	12	-24	3.91	3.37
		R insula lobe	32	22	-20	3.89	3.35
All cries > rest (+) with motor mask	44	L inferior frontal gyrus	-50	30	0	4.38	3.68
All cries > rest (+) with TOM mask	31	R insula lobe	32	22	-20	3.89	3.36
		R inferior frontal gyrus	32	16	-22	3.83	3.32
	32	L inferior frontal gyrus	-50	28	-2	3.85	3.33

A significant negative correlation between cerebral activity to crying and individual performance on authenticity ratings on crying was identified in bilateral precuneus, right superior frontal gyrus (BA 6), left MFG, left SFG, right IPL, and right middle occipital gyrus. Among these regions, the right SFG was found to be both activated by both the motor task and the TOM task, and the right IPL was only identified by the orofacial movement mask. On the other hand, bilateral precuneus, left MFG, and the L SFG were on other hand only identified by the TOM task (Fig. 6.23, Table 6.20).



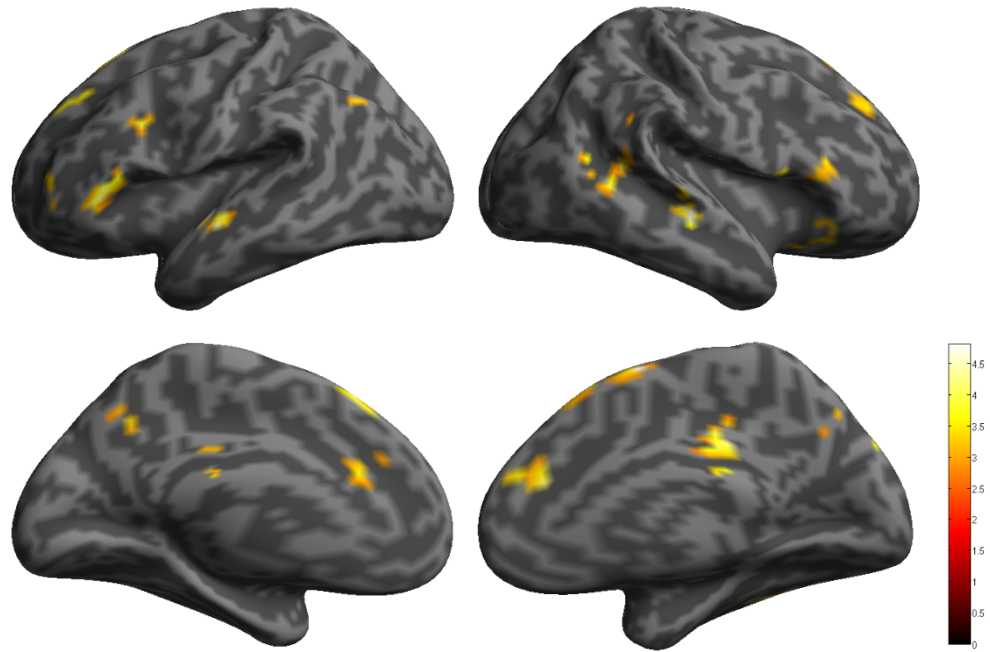
*Figure 6.23 Brain activations identified in the contrast of hearing crying against rest negatively correlated with the performance on the authenticity ratings on crying*

Table 6.20 Brain regions showing significant negative correlation between the performance on authenticity ratings on crying and the activations during the contrast of crying against silent rest, with inclusively masked by the contrast of motor and TOM task.

Contrast	No. of voxels	Region	x	y	z	T	Z
All cries > rest (-)	355	R inferior parietal lobule	36	-42	46	5.08	4.09
	1125	R superior frontal gyrus (BA 6)	26	8	64	5.03	4.06
	795	L middle frontal gyrus	-32	28	54	4.10	3.49
		L superior frontal gyrus (BA 6)	-16	6	56	3.79	3.29
	1835	L precuneus	-6	-62	50	4.57	3.79
		R precuneus	10	-66	52	4.55	3.78
	142	R middle occipital gyrus	38	-84	30	3.85	3.33
All cries > rest (-)	318	R inferior parietal lobule	36	-42	46	5.08	4.09
with motor mask	65	R superior frontal gyrus (BA 6)	30	-4	60	4.00	3.43
		R superior frontal gyrus (BA 6)	32	2	66	3.71	3.24
All cries > rest (-)	179	L precuneus	-6	-62	50	4.57	3.79
		R precuneus	4	-64	50	3.89	3.36
with TOM mask	142	R superior frontal gyrus (BA 6)	20	24	60	4.45	3.72
	102	L middle frontal gyrus	-32	28	52	3.97	3.41
	16	L superior frontal gyrus (BA 6)	-20	16	60	3.49	3.08

### 6.3.7.2 Covariate with contagion scores

A regression analysis was performed to examine the relation between cerebral activity to the perception of laughter and personal measures on the emotional contagion scale. The regression analysis on the contrast Laughter>rest identified activations in the bilateral IFG, bilateral MTG, bilateral STG, bilateral SFG, right posterior medial frontal gyrus (BA 6), right cuneus, bilateral precuneus, left cerebellum, right mid-cingulate cortex (MCC), left MFG, bilateral anterior cingulate gyrus (ACC), right fusiform gyrus, and left angular gyrus which were positively correlated with emotional contagion scores (Fig. 6.24, Table 6.21). In the contrast of hearing laughter against rest, no activation was found to be negatively correlated with emotional contagion scores.



*Figure 6.24 Brain regions which showed positive correlation between the contrast of hearing laughter against rest and emotional contagion measures.*

Table 6.21 Brain regions showing significant positive correlation between the performance on authenticity ratings on laughter and the activations during the contrast of hearing crying against silent rest, inclusively masked by motor and TOM task.

Contrast	No. of voxels	Region	x	y	z	T	Z
All laughs > rest	677	R inferior frontal gyrus	30	18	-24	6.71	4.90
	179	R superior temporal gyrus	56	-22	-2	5.75	4.45
	938	L middle frontal gyrus	-36	58	20	5.55	4.34
		L inferior frontal gyrus	-54	40	2	4.92	4.00
	153	L superior temporal gyrus	-54	-12	-6	5.18	4.14
	93	L superior frontal gyrus	-18	42	36	5.04	4.06
	259	L superior medial gyrus	-6	32	52	4.82	3.94
	155	R p-medial frontal cortex (pre-	8	4	68	4.67	3.85
	408	R middle frontal gyrus	56	-52	12	4.60	3.81
		R superior temporal gyrus	44	-44	16	3.92	3.38
	361	R cuneus	12	-86	44	4.33	3.64
		R precuneus	2	-66	40	3.75	3.26
		L precuneus	-4	-54	44	3.50	3.09
	174	L cerebellum	-24	-78	-30	4.28	3.61
	316	R middle cingulate cortex	8	-28	36	4.27	3.60
	222	L inferior frontal gyrus	-36	16	32	4.12	3.51
		L middle frontal gyrus	-28	18	34	3.63	3.18
	188	R anterior cingulate cortex	12	38	20	4.05	3.47
		R superior medial gyrus	10	50	24	3.65	3.19
	204	L anterior cingulate cortex	-4	30	30	3.96	3.41
	155	R superior frontal gyrus	16	42	34	3.96	3.40
		R middle frontal gyrus	26	48	26	3.02	2.73
	93	R fusiform gyrus	42	-46	-22	3.94	3.39
120	L angular gyrus	-36	-60	38	3.74	3.26	
All laughs > rest with motor mask	138	R p-medial frontal cortex	8	4	68	4.67	3.85
246	L inferior frontal gyrus	-52	26	0	4.33	3.64	
	L insula lobe	-46	6	0	3.06	2.77	
	L temporal pole	-48	10	-2	3.02	2.73	
279	R temporal pole	40	20	-24	4.03	3.45	
12	R posterior-medial frontal gyrus	-50	-6	-2	3.73	3.25	
75	R middle temporal gyrus	58	-58	10	3.64	3.18	
13	R cerebellum	40	-46	-26	3.54	3.12	
All laughs > rest with TOM mask	86	R inferior frontal gyrus	32	18	-24	6.32	4.72
	167	R superior temporal gyrus	56	-22	-2	5.75	4.45



88	L superior temporal gyrus	-54	-12	-6	5.18	4.14
91	L superior medial gyrus	-6	32	52	4.82	3.94
358	R middle temporal gyrus	56	-52	12	4.60	3.81
	R superior temporal gyrus	44	-44	16	3.92	3.38
172	L cerebellum	-24	-78	-30	4.28	3.61
37	L inferior frontal gyrus	-50	28	0	4.28	3.61
89	R posterior-medial frontal	10	24	58	4.03	3.45
214	R precuneus	2	-66	40	3.75	3.26
	L precuneus	-4	-54	44	3.50	3.09
	L posterior cingulate cortex	-4	-48	30	3.09	2.79
39	R superior frontal gyrus	16	46	34	3.72	3.24
47	R superior medial gyrus	10	50	24	3.65	3.19
	R anterior cingulate cortex	12	44	22	3.54	3.12
72	L angular gyrus	-44	-66	42	3.39	3.01
54	R inferior frontal gyrus	54	28	14	3.35	2.98

Another regression analysis was performed to examine the relation between cerebral activity to the perception of crying and personal measures in the emotional contagion scale. The regression analysis on the contrast Crying>rest identified activations in the bilateral IFG, right insula lobe, right STG, left STG, right posterior medial frontal gyrus (BA 6), and right superior medial gyrus which were positively correlated with emotional contagion scores (Fig. 6.25, Table 6.22). Among these regions, the right STG was further inclusively identified by the TOM task, and the right IFG was inclusively identified by the motor task. The left inferior occipital gyrus was found in the contrast of hearing crying against silent rest to be negatively correlated with emotional contagion score.

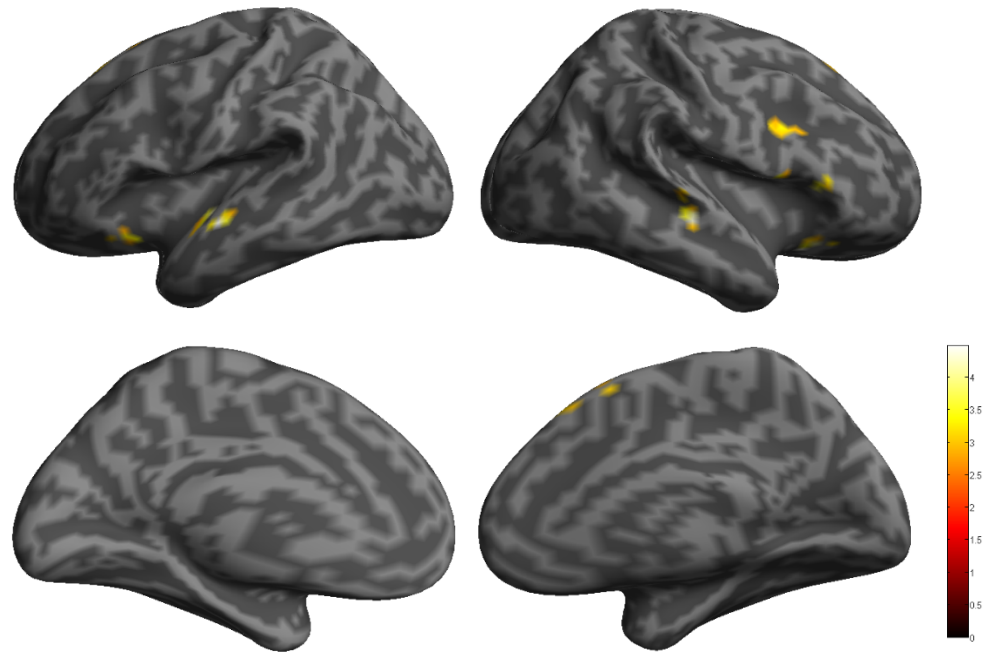


Figure 6.25 Brain regions which showed positive correlation between the contrast of hearing crying against rest and emotional contagion measures.

Table 6.22 Brain regions showing significant positive and negative correlation between the performance on authenticity ratings on crying and the activations during the contrast of hearing crying against silent rest.

Contrast	No. of voxels	Region	x	y	z	T	Z
All cries > rest (+)	117	R insula lobe	28	20	-18	5.40	4.26
	114	R superior temporal gyrus	56	-24	-2	5.00	4.04
	164	L Superior temporal gyrus	-54	-12	-6	4.55	3.78
	84	L inferior frontal gyrus	-30	22	-18	3.94	3.39
	82	R p-medial frontal gyrus (pre-SMA)	8	20	58	3.76	3.27
		R superior medial gyrus	10	32	54	3.61	3.16
	148	R inferior frontal gyrus	48	24	4	3.76	3.27
	109	R inferior frontal gyrus	38	10	28	3.40	3.01
All cries > rest (-)	103	L inferior occipital gyrus	-46	-62	-14	4.22	3.57

## 6.4 Discussion

### 6.4.1 Perception of laughter and crying

The network including the bilateral superior temporal gyri (STG), left middle frontal gyrus (MFG), left inferior frontal gyrus (IFG), bilateral precentral gyri, and left postcentral gyrus which was identified in the contrast of hearing all laughter and crying against resting baseline has been reported in previous studies when participants perceived non-verbal emotional vocalisations (Grandjean et al., 2005; McGettigan et al., 2015; Meyer, Zysset, Von Cramon, & Alter, 2005; Warren et al., 2006). It has been suggested that the network can be an auditory-motor ‘mirror’ system which is recruited in the perception of emotional vocalisations (Warren et al., 2006), and these activations are proposed to be simulated in the associated action for understanding others’ emotional states (Scott et al., 2009). In the current study, by applying the orofacial movement localizers (i.e., the motor mask) and the theory of mind localizers (i.e., the TOM mask), we can further explore the extent to which the two systems contributed to the perception of emotional vocalisations.

Perceiving laughter and crying recruited highly similar brain regions inclusively masked by the motor task, such as the upper bank of the bilateral STS, left Heschl’s gyrus, right IFG, right precentral gyrus, and bilateral cerebellum. The upper bank of the bilateral STS and left Heschl’s gyrus were repeatedly reported in previous studies to be activated by a perceived voice. They not only contribute to speech perception or to speech comprehension (Binder et al., 2000; Meyer, Alter, Friederici, Lohmann, & von Cramon, 2002; Meyer et al., 2005; Rodd, Davis, & Johnsrude, 2005) but are also associated with emotional prosody processing (Kotz et al., 2003). The STG is further suggested to be involved in extracting emotional information from vocal cues regardless of task demands and attention focus (Brück, Kreifelts, & Wildgruber, 2011). For example, the area was found to be more activated while listening to sentences during emotional compared to grammatical classification tasks (Beaucousin et al., 2007, 2011), and the area was also found to be sensitive to different auditory emotional categories (i.e., anger, sadness, joy, neutral, and relief) by showing distinct spatial patterns in response to each category compared to the others (Ethofer, Van De Ville, Scherer, & Vuilleumier, 2009). The right IFG identified in the current network is

also consistent with previous findings which suggested this area is highly correlated with emotion sensitivity (Kreifelts et al., 2013). This area along with the right STG were further suggested to be involved in decoding affective prosody and to evaluate emotional information delivered by speech (Brück, Kreifelts, Kaza, Lotze, & Wildgruber, 2011). Activation of the right precentral gyrus further replicates previous findings that the area was a common area activated by perceiving emotional vocalisations (i.e., triumph, fear, amusement, disgust) and an orofacial movement task (Warren et al., 2006), and the area was also found to be activated by speech perception and speech production (S. M. Wilson, Saygin, Sereno, & Iacoboni, 2004). The current study again suggests an existing link between perception and action in the processing of emotional vocalisations.

While applying the TOM mask, the network of perceiving laughter and crying showed a highly similar profile to the regions mentioned above, including the right IFG, the bilateral cerebellum, and the bilateral STG. However, instead of involving sensorimotor regions (i.e., precentral and Heschl's gyrus), the lower bank of the bilateral STG, right STS, and left MTG were identified in the theory of mind network as common areas while listening to laughter and crying. As mentioned earlier, STG has been reported to be sensitive to human voice, and right STG was also reported to be involved in decoding, extracting, and evaluating emotion information carried by speech. Previous evidence further showed that activations in the right STG extending to the right STS can be involved in affective theory of mind network (affective TOM) (Mier et al., 2010). In the study conducted by Mier et al. (2010), participants were required to read a sentence stating a possible description of a corresponding photograph of a facial expression, and then the participants responded 'Yes' or 'No' to the photograph based on the antecedent description. The sentence was in one of the three conditions: emotion recognition, affective TOM, and control. The participants were asked to judge whether the facial expression matched the description of emotion, the action described according to each of the affective states (i.e., joy, fear, anger, disgust), or the sex of the person. Several regions were activated by the affective TOM compared to the emotion recognition, including the bilateral MTG, right STG, bilateral STS, right inferior parietal lobule, and angular gyrus. These brain areas were argued to serve as a simulation mechanism for

understanding the emotional intention of others (Mier et al., 2010). In the current experiment and in line with previous findings, we demonstrated that passively perceiving laughter and crying can automatically involve several regions identified by the TOM network and the motor network, implying that some parts of the two networks can be automatically recruited for emotional auditory processing.

#### 6.4.2 Perceiving involuntary vocalisations over voluntary vocalisations

##### *Laughter (involuntary > voluntary)*

When comparing involuntary vocalisations over voluntary vocalisations in perceiving laughter, activations in bilateral STG and right rolandic operculum were identified in the motor mask. The activation in bilateral STG replicated previous findings that the regions were more activated by evoked laughter (i.e., involuntary laughter) compared to emitted laughter (i.e., voluntary laughter) (McGettigan et al., 2015). The right STG was also identified to show greater activation for ticklish laughter than for other kinds of laughter (i.e., joy and taunt) (Szameitat et al., 2010). The areas we identified here provides further evidence that perceiving involuntary or ticklish laughter compared to voluntary laughter can elicit more activations in the STG inclusively masked by the orofacial movement task.

While applying the TOM mask to the contrast of hearing involuntary laughter over voluntary laughter, the posterior part of the right STS (i.e.,  $x = 46$ ,  $y = -42$ ,  $z = 14$ , BA 22) was identified. The posterior part of the right STS towards the middle STS has been suggested to be a voice-selective area (Bethmann & Brechmann, 2014), and activation in the right pSTS was further reported to be associated with ability to detect perceived authenticity in laughter (McGettigan et al., 2015). Additionally, the region was consistently reported to be sensitive to visual cues in social perception such as direction of eye gaze, body motions, or lip reading (Allison, Puce, & McCarthy, 2000). Converging with previous findings, the right pSTS here showed greater activation while perceiving involuntary laughter compared to voluntary laughter under the TOM mask,

which may imply that an automatic process of motion perception was involved in perceiving contagious laughter.

#### *Crying (involuntary > voluntary)*

The left posterior middle temporal gyrus (pMTG) was the only area which showed more activation for involuntary crying than for voluntary crying and was neither identified during the motor task nor in the TOM task. Although a nearby region previously identified by affective TOM task compared to emotion recognition task showed more involvements of mentalising others' affective states (Mier et al., 2010), the region we found in the current contrast relatively infrequent to be associated with emotion related studies. In a recent meta-analysis, the bilateral pMTG were reported to be more involved in affective TOM network compared to cognitive network (Molenberghs, Johnson, Henry, & Mattingley, 2016). However, the authors concluded that especially the left pMTG was mainly reported to be involved in the language comprehension process by extracting semantic information from TOM stories, so the activation of this region had only little relation to mentalising ability. Indeed, the left pMTG was consistently reported to be a crucial area for storing, selecting, and analysing semantic representation (Rapp, Mutschler, & Erb, 2012). Another meta-analysis study found that instead of reappraisal of emotion engaging the ventromedial prefrontal cortex, the lateral middle temporal gyrus played an important role in re-evaluating affective information. This region might be recruited to reconstruct the negative emotional information for reducing affective impact (Buhle et al., 2014). In line with these interpretations, the activity in the left pMTG can imply that the participants might be engaged in the emotion regulation process while perceiving involuntary crying sounds compared to voluntary crying sounds.

#### **6.4.3 Perceiving voluntary vocalisations over involuntary vocalisations**

##### *Laughter (voluntary > involuntary)*

When comparing voluntary vocalisations over involuntary vocalisations in perceiving laughter, the left angular gyrus was identified in the TOM mask and

no common area was identified in the motor mask. We identified the left angular gyrus to be more activated by voluntary over involuntary laughter located at the temporal-parietal junction (TPJ) which was consistently reported in the TOM network (Atique, Erb, Gharabaghi, Grodd, & Anders, 2011; Hervé et al., 2013; Saxe & Kanwisher, 2003). The area was suggested to be involved in reasoning others' mental states, and the left TPJ compared to the right TPJ was less associated with simulating body movements and perceiving photographs of human bodies. On the other hand, the left TPJ was proposed to be relatively sensitive to 'verbal descriptions' of the context compared to the right TPJ (Saxe & Kanwisher, 2003). In another study, although the bilateral TPJ were both activated to make inferences of emotions or intentions of cartoon characters compared to physical reasoning, the left TPJ showed significant spatial distances between peak activations of the two mentalising tasks (Atique et al., 2011). In the current contrast, the activation of the left TPJ can be explained by involving a reasoning process while the participants perceived voluntary laughter, however it is unclear whether the participants were inferring the intention or the emotion of the speakers through our stimuli. McGettigan et al. (2015) examined the same cluster and reported that the region showed significant correlation between neural activations of perceiving laughter and the ability to detect authenticity in perceived laughter. In line with previous findings, the activation of the left TPJ identified in the current contrast may imply that a mentalising process of reasoning others' emotion or intention while they were producing voluntary laughter might be engaged to differentiate voluntary laughter from involuntary laughter.

#### *Crying (voluntary > involuntary)*

When comparing voluntary crying to involuntary crying, the bilateral STG, left Heschl's gyrus, right thalamus, right precentral gyrus, right MFG, and right temporal pole were identified in the motor mask, while the bilateral STG and bilateral MTG were identified in the TOM mask. Here we demonstrated a highly similar profile of regions which were identified previously by perceiving laughter and crying over the resting baseline. However, the right thalamus, the right MFG, the right temporal pole, and bilateral MTG were additionally involved in

perceiving voluntary crying. Yet, little is known about the brain activations for perceiving adult crying, and the regions we identified in this contrast can be involved in a general network of perceiving emotional vocalisations, in which the motor and theory of mind related regions were recruited for the perception of crying sounds. Voluntary crying might be relatively infrequently heard in everyday life, however the occasion of hearing it might indicate that someone is sending compelling signals that they are in vulnerable and need attentions from others (Hendriks et al., 2008). It is possible that extensive regions of the two networks were recruited for the purpose of trying to understand these crying sounds.

#### 6.4.4 Individual differences in perceiving emotional vocalisations

Cohen's *d* scores were first calculated for each participant based on the rating results of perceiving authenticity in laughter and crying respectively. The scores of Cohen's *d* showed to what extent the participant could differentiate involuntary vocalisations from voluntary vocalisations, representing the psychological distance of perceived authenticity between involuntary and voluntary vocalisations. In an individual differences approach, whole-brain second-level regression analyses explored the relationship between the ability to differentiate vocalisations by perceived authenticity on the post-test and neural responses to laughter and crying in the passive listening phase of the fMRI experiment. A separate regression model was run for All Laughter (involuntary and voluntary) > Rest and All Crying (involuntary and voluntary) > Rest, using individual Cohen's *d* scores on laughter or on crying as the predictor variables in each case respectively.

##### *Laughter*

The regression analysis on the contrast All Laughter > Rest identified activations in the left supramarginal gyrus, left MTG, left angular gyrus, and right precentral gyrus which were positively correlated with behavioural performance. The left supramarginal gyrus including the posterior part of the left MTG were inclusively masked by both the motor task and the TOM task, while the left



angular gyrus was only identified in the TOM task and the right precentral gyrus was only identified in the motor mask.

The left supramarginal gyrus and the precentral gyrus were commonly reported in motion-related studies, and since the areas were associated with execution of hand motion, observation of actions, and processing of goal-oriented body-part motion, they were proposed to be part of the ‘mirror system’ (Van Overwalle & Baetens, 2009). By being sensitive to body movements, the supramarginal and the precentral gyrus were suggested to together play crucial roles in the understanding of human actions, especially when the action is in relation to an antecedent cause or to a subsequent outcome.

The left supramarginal and the left angular gyrus were both identified in the TOM mask, and their activations showed positive correlation with the behavioural performance. These two regions were also reported in the study by McGettigan et al. (2015), showing significant positive correlation with participants’ performance on a post-scan task of classifying evoked laughter and emitted laughter. The reported areas were consistently involved in the affective and the cognitive TOM networks, however they were found to be more activated during cognitive TOM task (Molenberghs et al., 2016), suggesting that the involvements can be associated with mentalising ability to infer intentions, goals, or beliefs of others, rather than being associated with inferring others’ affective states.

The results indicated that the participants with better ability to perceive authenticity differences between involuntary and voluntary laughter can be associated with these two different neural networks. In addition, the more of the networks were involved, the more competent the participants in understanding laughter.

### *Crying*

Several regions had greater activations positively correlated with the performance on perceived authenticity between involuntary crying and voluntary crying. The results showed that the bilateral IFG, right temporal pole, and right insula lobe

were positively correlated to the performance. The left IFG was identified in both motor and TOM networks, and the right IFG and the right insula were only identified in the TOM network. Previous studies frequently found activations in the bilateral IFG for observing action as well as emotion-related and mentalising processing. The IFG, along with other regions including the dorsal and ventral premotor cortex and superior and inferior parietal lobule, were specifically suggested to serve as a core network of mirror properties processing (Molenberghs, Cunnington, & Mattingley, 2012). In the mirror system, the bilateral or unilateral IFG were further implicated to be involved in emotional empathy processing (Baird, Scheffer, & Wilson, 2011). Baird et al. (2011) argued that emotional empathy can only be driven by passively perceiving actions or expressions, in which the measures of automatic imitation in perceivers are considered to be the pure form of empathic functioning.

The ‘imitation effect’ is indeed the core concept of mirror neuron theory, and the effect was further adopted in explaining the perception of emotional expressions to which the perceiver can elicit similar or even identical emotional behaviour (e.g., disgust) (Wicker et al., 2003). It has been demonstrated in patient studies that the functions of IFG and the ventromedial prefrontal cortex (vmPFC) in empathising with others can be double dissociated. A patient with impairments in the IFG showed deficits in emotional empathy, and the other patient with lesions in vmPFC showed impaired ability of cognitive empathy. They both showed normal abilities of emotional or cognitive empathy according to the intact IFG and vmPFC respectively (Shamay-Tsoory, Aharon-Peretz, & Perry, 2009). Although in the current study we could not know whether the participants empathised with the speaker when they heard crying sounds, the increased activity of IFG associated with the ability of understanding crying sounds can suggest that the regions indeed advanced the ability to differentiate involuntary crying from voluntary crying.

Interestingly, a distinct profile of cerebral activity was found to be negatively correlated with the performance on the differences of perceived authenticity between involuntary and voluntary crying. The bilateral precuneus, bilateral superior frontal gyrus (SFG, BA 6), left MFG, right IPL, and right middle occipital gyrus were identified to show increased activity when the participants were less able to distinguish involuntary crying from voluntary crying

on the authenticity scale. Among these regions, the right SFG was found to be activated in both the motor mask and the TOM mask. The right IPL was only identified in the motor mask, while the bilateral precuneus, left MFG, and the left SFG were only identified in the TOM mask. Although identified in both or either of the networks, these areas were not the ‘core regions’ previously defined within each of the networks. On the other hand, these regions were identified as a network serving functions of ‘visual imagery’ (Zvyagintsev et al., 2013). In the study, activations in the bilateral SFG, the bilateral precuneus, and the bilateral MFG were found to be deactivated during auditory imagery tasks but more activated during visual imagery tasks. In the current study, it is possible that the poor performance in distinguishing involuntary crying from voluntary crying can be attributed to relying on visual imagery processing rather than using the mentalising and the orofacial movements network.

## 7. General discussion and conclusion

I will first summarise the main findings and provide plausible explanations of the current findings and then suggest a few research directions for future studies, which may be able to provide empirical corroboration of the explanations offered in the current thesis.

### *Authenticity perception of laughter and crying during childhood*

The motivation of the thesis was to investigate whether the difference in perceived authenticity between involuntary laughter and voluntary laughter demonstrated in the previous study (McGettigan et al., 2015) could be replicated and extended to the perception of negative emotional vocalisations—involuntary and voluntary crying. Using the difference of perceived authenticity between involuntary and voluntary vocalisations allowed me to explore potential similarities and differences between the perception of positive and negative emotional vocalisations—laughter and crying—in addition to their distinct valences. Previous findings have shown that listeners can accurately classify involuntary laughter from voluntary laughter when assessing authenticity. In this thesis, I investigated whether crying sounds share similar psychological properties with laughter, i.e., whether these involuntary vocalisations were perceived as more authentic and more contagious than voluntary vocalisations.

I first discovered that crying was perceived as more authentic when the speakers had less voluntary control. However I found, in the behavioural pilot experiments, that the perceived difference of authenticity between involuntary and voluntary crying vocalisations was reduced, relative to the perceived authenticity difference between voluntary and involuntary laughter. In addition,

crying sounds were perceived as less genuine than laughter. The focus was then expanded to the developmental learning trajectories of perceiving these two emotional vocalisations, after their initial development early in infancy. Perceived authenticity was found to be different between involuntary and voluntary vocalisations and that this difference increased with age. On the other hand, although laughter was perceived as more authentic than crying, the difference was shown to be similar in each age group.

The findings so far provide a valuable profile of the perception of laughter and crying from a developmental perspective. Firstly, involuntary and voluntary vocalisations can be distinguished based on involuntariness regardless of positive or negative emotional expressions throughout a lifetime. Secondly, although children rated involuntary vocalisations as less authentic and rated voluntary vocalisations as more authentic than did any other age groups, children can still perceive authenticity differences between involuntary vocalisations from voluntary vocalisations. Together, these findings might indicate that the sense of authenticity embedded in these two emotional vocalisations can be acquired quite early in life. It is possible that the perception of authenticity is tightly linked to other cognitive/affective abilities, such as verbal or linguistic ability, mentalising ability, or the concepts of understanding self and others, which develop rapidly throughout childhood. Another possibility which might contribute to the development of authenticity perception is that pre-schoolers or schoolers start to have more opportunities to interact with others than before, so a social learning process can take place to enhance the ability of differentiating vocalisations with distinct social meanings.

*The perception of voluntary vocalisations develops more slowly than that of involuntary vocalisations*

Involuntary laughter has a striking contagious influence on the perceivers. Contagious laughter has been depicted as an ancient and unique form of pre-linguistic auditory communication in humans (Provine, 1992), and my results in line with previous research demonstrate that involuntary laughter indeed has a robust contagious influence, even from three years of age observed in this experiment. Compared to involuntary laughter, voluntary laughter not only

followed a slower developmental trajectory on the perception of contagiousness, but the perceived authenticity of voluntary laughter also develops later. In line with previous findings (Lavan, Scott, & McGettigan, 2016; McGettigan et al., 2015), this later-developed ability to recognise the perceived authenticity of voluntary laughter can be linked to the development of the anterior medial prefrontal cortex, which was demonstrated to mature only during early adulthood (Gogtay et al., 2004). Voluntary laughter is also called conversational laughter or social laughter, which can convey very different meanings depends on distinct social contexts (Provine, 2012). To recognise the meanings of voluntary laughter and to decide whether it is appropriate to join in voluntary laughter may require mentalising ability in perceivers (McGettigan et al., 2015). Previous research suggests that the mentalising ability involves a complex process, including differentiating self from others, understanding social contextualised information, recognising emotions, and inferring others' cognitive or affective mental states (Hillis, 2014). These components may still be developing during adolescence that adolescents are accumulating social experience and learning social skills to confronting the changing environment (Burnett & Blakemore, 2009).

It is evident that the perceived contagiousness of voluntary crying also followed a slower developmental trajectory than that of involuntary crying. Although all age groups showed unwillingness to join in crying, this unwillingness was significantly demonstrated when they perceived voluntary crying across age groups. Children to some degree perceived voluntary crying as contagious, but the contagiousness decreased rapidly during adolescence. Moreover, the perceived contagiousness of voluntary crying was found to be different between adolescents and adults. It is possible that as we grow older, we learn more social rules of expressing sadness compared to when we were younger, so adults rated voluntary crying to be the lowest degree (i.e., 1.7 of 5) of perceived contagiousness among all other emotional vocalisations in the experiment. The protracted developmental trajectory followed by the perceived contagiousness of voluntary crying might imply that although crying can be a powerful emotional signal to the perceivers showing someone needs attention and assistance (Vingerhoets et al., 2000), whoever receives the signal may not share intentions of joining in. Crying behaviour is proposed to be an emotional reaction when individuals cannot use effective behaviour to confront a

problematic situation (van Hemert et al., 2011). Shedding emotional tears although is one way to express distress, it is not a conventional way of behaving in adults. There is a wide variety of reasons or situations which may cause adult crying (Vingerhoets & Bylsma, 2016), but hearing others' voluntary crying may not be one of the circumstances. That is, voluntary crying in adults is not a socially approved emotional expression. When perceiving socially inappropriate emotional displays, there can be stronger affective reactions shown in perceivers toward the displays (van Kleef, 2009). Therefore, the growing unwillingness observed in joining in voluntary crying across lifespan can be caused by aversive responses which are learnt from social contexts to this socially disapproval behaviour.

#### *Pupil dilation signals authenticity effect*

In the pupillometry experiment, I found a main effect of involuntariness on pupillary response showing that pupils dilated greater for perceiving involuntary emotional vocalisations than for voluntary ones, while pupillary responses showed no difference between perceiving laughter and crying. The behavioural results showed that participants perceived involuntary vocalisations as more authentic than voluntary vocalisations, but perceived crying sounds as less authentic than laughter.

The discrepancy found in our research between pupillometry and the conscious ratings of crying sounds may be caused by display rules prescribing appropriate ways of expressing emotions. Because crying as an intense emotional expression may cause receivers to experience a negative emotional state, the reaction of receivers to a crying person may be influenced by social factors which are specifically rigid for crying behaviour (Simons, Bruder, van der Löwe, & Parkinson, 2012; Vingerhoets et al., 2000). For example, receivers who hear crying sound may try to manage an appropriate responsive behaviour toward the person who sheds tears or to regulate their own affected emotional states cognitively. From perceiving an emotional crying sound to making a cognitive judgement on whether the sound reflects a genuine emotion, a series of psychological process might be involved (Mitchell & Phillips, 2015). For example,

top-down mechanisms based on receivers' long-term knowledge of reacting to a crying adult can influence their judgements on emotional expressions. It is also possible that recognising a person who is genuinely expressing sadness requires more information about the person, about the social contexts, or even requires visual information such as appearance of emotional tears. The perception of adult crying remains an elusive process that needs more empirical evidence for better understanding.

### *The perception of involuntary crying and display rules*

For the perceived contagiousness of involuntary crying, children and adolescents showed no difference from each other, but children significantly rated involuntary crying as more contagious than did adults and young adults. Furthermore, adolescents showed more willingness to join in involuntary crying vocalisations than adults did. It has been proposed that adolescence is a time of transition from childhood to adulthood by showing hypersensitivity to sociocultural information (Blakemore & Mills, 2014). This hypersensitivity found in adolescents can be closely related to the ability to empathise others. Sebastian et al. (2012) observed an increased activation in ventral medial prefrontal cortex (vmPFC) in adolescent group when performing an affective TOM task compared to a physical causality task requiring participants to reason the cause and effect of events. There was also a negative correlation between brain activation in the frontal control region (i.e., ventrolateral PFC) and empathy scores, showing that individuals with better ability to reasoning others' affective mental states may have less difficulty to regulate their own emotions induced by others.

The unwillingness to join in involuntary crying demonstrated in adults provides supportive evidence in line with previous research that although crying adults can sufficiently solicit perceivers' willingness to help (Hendriks et al., 2008), and tearful faces were seen as warmer than non-tearful sad faces, tearful faces were perceived as less competent than non-tearful sad faces (van de Ven et al., 2017). It is possible that expressing negative emotions by shedding tears or weeping is viewed as a sign of weakness in personality (Tseng, 2001) which caused participants unwillingness to join in. It remains elusive that whether



participants felt any negative emotions (i.e., sadness or distress) while perceiving involuntary crying, and whether they perceived speakers who had produced involuntary crying as less competence. There are other explanations of why adults refused to join involuntary crying. It is possible that perceiving sadness can be linked to empathy processing and the perceivers regulated this negative emotion cognitively (Harrison et al., 2007; Williams & Morris, 1996). Therefore, although they perceived involuntary crying as more authentic than voluntary crying, they showed less intention to join in.

### *Neural correlates of the perception of laughter and crying*

I found a brain network of perceiving laughter and crying similar to that was identified when participants passively listened to laughter (McGettigan et al., 2015), and also demonstrated the involvement of bilateral temporal cortices during the perception of involuntary laughter compared to voluntary laughter, in line with previous studies (Lavan et al., 2016; McGettigan et al., 2015). Moreover, I replicated the involvements of sensorimotor regions positively correlated with authenticity perception on laughter (McGettigan et al., 2015). In addition, I demonstrated involvement of the right precentral gyrus which showed positive correlation between the activation of perceiving laughter against the resting baseline and authenticity perception on laughter, which also supports the idea that perceiving positive emotional vocalisations induce sensorimotor activations (Warren et al., 2006).

However, I did not observe activations of the amPFC in the contrast of perceiving voluntary laughter against involuntary laughter. Instead, I observed greater activation of the left angular gyrus for perceiving voluntary laughter compared to involuntary laughter. Activations of this area was positively correlated with authenticity perception of laughter. The area has been shown to be involved in the theory mind network (Hervé et al., 2013).

In the analyses of individual differences of perceiving crying, I found a brain network negatively correlated with authenticity perception of crying. The network can be related to self-perception or visual imagery (Kestemont et al., 2015; Zvyagintsev et al., 2013), however, it needs following analysis or

experiments for further understanding the mechanism of this network. It is possible that the identified network can provide novel insights for why participants performed poorer authenticity judgements on the perception of crying compared to laughter.

### *Limitations for the study and future directions*

In the current study, although laughter and crying are considered as social emotional expressions, there is no explicit tasks for pinpointing distinct social information processing in perceiving these emotional vocalisations. It is worth conducting further experiments to understand how the perception of involuntary/voluntary laughter and crying may influence cognitive or affective processing in perceivers' minds. Perceiving, recognising, interpreting, and empathising emotions expressed by others can be distinct processes which can also interact with different social contexts in various ways. It would be valuable to understand underlying mechanism and to clarify how the perception of authenticity and contagiousness changes under different situations or on individuals with different types of personalities.

For the developmental perspective of emotion processing, although the current experiment provides cross-sectional results across age groups and shows distinct developmental trajectories on the perception of involuntary and voluntary emotional vocalisations, it is worth conducting a longitudinal study where the developmental changes are tracked in the perception of laughter and crying as people get older, and see how these scores relate to other measures.

In the current fMRI experiment, there were two localisers applied (i.e., orofacial movement localiser and TOM localiser). However, these two networks showed partial overlapping regions which were not distinct enough, and it is also failed to include much activation of medial prefrontal areas in the TOM localiser. There is also no evident neural activation found to be differed between valence of emotions (i.e., laughter and crying) and authenticity regardless of emotions (i.e., involuntary and voluntary). This could be due to that emotions processing in the brain may not be differentiated by these dimensions. The difference of perceived authenticity is shown in the pupil response to laughter and crying, it is

worth understanding how this physiological response link to brain activation, and how it would enrich our knowledge of emotion processing from physical level to neural level.

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