



## The role of external factors in affect-sharing and their neural bases

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### ABSTRACT

Affect-sharing, the ability to vicariously feel another person's emotions, is the primary component of empathy that is typically thought to rely on the observer's capacity to feel the emotions of others. However, external signals, such as the target's physical characteristics, have been demonstrated to influence affect-sharing in the neuroscientific literature that speaks to the underappreciated role of external factors in eliciting affect-sharing. We consider factors that influence affect-sharing, including physical cues, emotional cues, situational factors, and observer-target relationships, as well as the neural circuits involved in these processes. Our review reveals that, while neural network activation is primarily responsible for processing affect-sharing, external factors also co-activate a top-down cognitive processing network to modulate the conscious process of affect-sharing. From this knowledge, an integrative framework of external factor interactions with affect-sharing are explained in detail. Finally, we identify critical areas for future research in social and affective neuroscience, including research gaps and incorporation of ecologically valid paradigms.

### 1. Introduction

Empathy reflects the capacity to experience and understand the thoughts and emotions of another person. It is a core aspect of human social cognition that plays an essential role in social interactions (Decety and Jackson, 2004; Henry et al., 2016) and is therefore integral to our emotional well-being (Weisz and Cikara, 2021). Conversely, atypical empathic processing contributes to social dysfunction and makes it more difficult to develop strong and stable interpersonal relationships (Dziobek et al., 2008).

In the last 20 years, substantial attention has focused on understanding the psychology and the neural bases of empathy. Yet a striking feature of this literature is that, although empathy reflects an interpersonal process between an observer (the individual focusing on the subjective state of another person) and a target (the individual who is the focus of the observer's attention), almost all research to date has concentrated on how observer traits and cognitions modulate empathic processing. Comparatively, there has been limited attention on the characteristics of target and external factors that influence the generation of empathy in observers.

Although there has been an earlier review into empathy as dependent on situational-contextual factors that is not automatically elicited (Hein and Singer, 2008), this evaluation was brief due to the paucity of

early research. This current paper addresses this gap in the literature by summarising evidence from the past 15 years to provide a clearer and more comprehensive understanding of neuroscientific literature that accounts to how external factors influence the elicitation of affective empathy in observers and the neural mechanisms that underpin these behavioural effects.

This paper is a narrative review, with publications found using the search string "(affective empathy OR affect-sharing OR experience-sharing) AND (neural OR neuroscience OR neuroimaging)". From this, papers were screened based on their abstracts and included if they were empirical papers that directly measured state affective empathy or neural empathic activity, and included some manipulation or quasi-experimental measurement of an external factor that influenced state empathy and/or neural empathic activity. Papers were excluded if they were duplicates, not written in English, did not involve human participants, were narrative or systematic review papers without empirical findings (meta-analyses were included in the search, but not treated as primary sources) or did not manipulate or measure state empathy, such as papers that only measured trait empathy. Neuroscientific papers involving the measurement of neural empathic activity were the primary focus of this review, but psychological studies were also included if the neuroscientific evidence for a specific external factor was absent.

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### 1.1. Defining empathy

Empathy consists of three distinct but interrelated components: perspective-taking, affect-sharing (affective empathy) and empathic concern (Decety, 2015; Weisz and Cikara, 2021). Although there are competing views on how these components should be described, in the present review, we define *perspective-taking* as the ability of an observer to adopt and understand the psychological perspective of another person, *affect-sharing* as the ability to share the emotional states of others and *empathic concern* as the motivation to promote the wellbeing of others (Bernhardt and Singer, 2012; Shamay-Tsoory, 2011; Walter, 2012; Weisz and Cikara, 2021). A real-world example that might trigger these components of empathy is watching someone cry. Although you can see and understand that they are sad without necessarily feeling sad yourself, watching someone cry may make you feel sad and want to alleviate that person's suffering. Although there is considerable variance between neurotypical individuals in how adept they are at understanding others' sadness, how readily they will experience feelings of sadness themselves and how much they want to help that person in their sadness, these processes are indicative of the distinct psychological concepts of perspective-taking, affect-sharing and empathic concern, respectively, and their related processes.

Perspective-taking overlaps conceptually with mentalising, which is the capacity to consciously understand the mental states of oneself and of others (Gallagher and Frith, 2003; van Overwalle and Baetens, 2009). Specifically, the capacity for mentalising is required for perspective-taking, as understanding the cognitive states of others is needed for perspective-taking (Hooker et al., 2010). Importantly, mentalising is also distinct from affect-sharing. Whereas mentalising may impose substantial demand on controlled, cognitive processing without invoking the emotions of others in the self, affect-sharing reflects bottom-up processing associated with affect-sharing and affective responsiveness to the emotions of others (Decety and Lamm, 2006; Hooker et al., 2010).

A key component of perspective-taking and affect-sharing is a self-other distinction, which refers to the capacity to distinguish between one's thoughts, affect and actions and those of others (Decety and Jackson, 2004, 2006; Decety and Lamm, 2007; Lamm et al., 2016; Walter, 2012). This mechanism is necessary to prevent egocentric bias – the projection of one's mental states onto others – when assessing the internal states of others. Suppression of this bias, therefore, promotes more accurate appraisals of the feeling states of others and, therefore, more appropriate empathic responses to them (Mitchell, 2009; Silani et al., 2013).

This self-other distinction differentiates affect-sharing from other affective phenomena such as emotional contagion (the tendency to feel the emotions of another person automatically; Hatfield et al., 1993) as well as personal distress (the negative affective state elicited from the usually negative affective state of others; Davis, 1980), neither of which require explicit self-other distinction (Decety and Lamm, 2009; Walter, 2012).

Due to empathy's multifaceted structure, there is ongoing debate over its precise definition. Some researchers have defined empathy as purely to affect-sharing (e.g., Singer and Lamm, 2009) while others emphasised affect-sharing and perspective-taking as the key components of empathy (e.g., Decety and Jackson, 2004). For the purposes of this review, we will use the three-component model of empathy described previously. Without focusing too heavily on the phenomenology and semantics of empathy, this review uses the working definitions of perspective-taking as the capacity to adopt and understand the thoughts and perspectives of another and affect-sharing as the ability to share the emotional states of others, and it is this latter component of empathy that is of central interest in this paper.

### 1.2. Testing and measuring affect-sharing

Studies that modulate state affect-sharing typically involve the presentation of stimuli selected to evoke a specified emotion and then measure the degree to which observers share the target's emotions. Commonly used stimuli include the presentation of emotional facial expressions, physical sensation that imply the expression of a specified emotion, or descriptive vignettes of targets experiencing a specified emotion. A major subset of affect-sharing studies uses the empathy-for-pain methodology, which assesses vicarious negative affect felt by an observer watching a target experiencing pain (for review, see Lockwood, 2016). The ubiquitous nature and salience of pain provide researchers with a predictable platform for inducing affect-sharing that captures the observer's attention and directs it to the empathic stimuli.

As first documented by Singer et al. (2004), although observing the pain of others activates the affective-motivational component of the pain response but not the sensory component of pain, there is nevertheless significant neural overlap between empathic pain and the firsthand experience of pain (Jackson et al., 2005; Morrison et al., 2004; Zaki et al., 2007; Lamm et al., 2011). Causal evidence for this phenomenon was established with psychopharmacological research using analgesics to suppress the firsthand experience of pain, such that inhibiting firsthand pain using a placebo analgesic reduced neural empathic activation and subjective empathy for a target's pain (Rütgen et al., 2015) and empathy for unpleasant touch (Rütgen et al., 2021), which can then lead to a downstream reduction in prosocial helping of others in pain (Hartmann et al., 2022). The administration of painkillers such as paracetamol also decreased neural and subjective empathy for pain (Mischkowski et al., 2016) and empathic feelings for another's positive emotions (Mischkowski et al., 2019). Additionally, recent research employing hypnosis found that the experimental reduction of pain using hypnotic suggestion decreased subjective and neural empathy for pain (Braboszcz et al., 2017), and hypnotic induction of affect-sharing increasing vicarious fear learning compared to low affect-sharing (Müllner-Huber et al., 2022).

Although affect-sharing can be operationalised and measured using self-report, behavioural tasks and electrophysiology (for review, see Neumann and Westbury, 2011), the principal focus of this review will be studies that have assessed affect-sharing using neuroimaging paradigms. In this literature, when higher self-reported or behavioural task performance scores are associated with increased activation in regions of interest (ROIs) for both vicariously experiencing an emotion and its firsthand experience, this is interpreted as heightened affect-sharing for the target. Research in the past ten years has moved away from univariate ROI magnitude response for firsthand and vicarious emotions, to using multivoxel pattern analysis (MVPA), a sophisticated neuroimaging analysis technique that measures variable patterns of neural activation across different voxels (Haxby et al., 2001; Weaverdyck et al., 2020). In a seminal study by Corradi-Dell'Acqua et al. (2016) using MVPA to systematically investigate similarities and differences in firsthand and empathic responses to pain and disgust, some brain regions were found to activate for modality-independent affective unpleasantness but other regions activated only for modality-specific. Another study using the same method of analysis to investigate similarities and differences for pain on body parts and painful facial expressions found an overlap in brain regions involved in cross-modal empathic processing of pain that was not sensitive to non-painful negative stimuli (Zhou et al., 2020). Indeed, recent neuroimaging research has shifted toward investigating functional networks involved in affect-sharing (Ebisch et al., 2022; Maliske and Kanske, 2022), including with MVPA (Berluti et al., 2020; O'Connell et al., 2019). Combining neuroimaging and behavioural techniques can provide unique insights into state affect-sharing by allowing the interaction between explicit affective resonance and implicit processing to be directly assessed.

### 1.3. Neural substrate of affect-sharing

Research investigating empathy in social, cognitive and affective neuroscience has established that affect-sharing and perspective-taking depend on the activity of distinct neuroanatomical regions that act in concert as dissociable functional networks (Eres et al., 2015; Valk et al., 2017).

Most of the early evidence investigating empathy for others indicates that the anterior insula (AI) and anterior cingulate cortex (ACC) comprise an important network of affect-sharing (Engen and Singer, 2013; Lamm et al., 2011; Timmers et al., 2018; Wang et al., 2014), with one meta-analysis specifically implicating the bilateral AI and dorsal ACC (dACC) as a key affect-sharing nodes primarily for pain and negative emotions such as sadness and disgust (Fan et al., 2011). Critically however, this research was biased towards empathy for pain and other negative emotions, with different regions activated during empathy for positive emotions (Morelli et al., 2014). The dACC and the anatomically proximate anterior mid-cingulate cortex (aMCC) have been shown to encode the affective component of physical pain (Price, 2000) and process socio-affective information through its engagement during social evaluation and social exclusion (Eisenberger et al., 2003; Kawamoto et al., 2015). The dACC is also thought to be a neural hub for integrating negative affect, pain and cognitive control for adaptive threat response (Shackman et al., 2011) and contains efferent connections to the AI (Allman et al., 2010; Craig, 2009). The right AI integrates bottom-up interoceptive signals with top-down information to contribute to the conscious awareness and representation of affective states and has been identified as the neural basis for the abstract representation of the self (Carr et al., 2003; Craig, 2009; Critchley et al., 2004; Gu et al., 2013). Activation of the right AI also correlates with self-reported affect-sharing (Kanel et al., 2019). The left AI is engaged when experiencing firsthand disgust and viewing disgusted facial expressions (Wicker et al., 2003). However, while the bilateral AI is activated for firsthand and vicarious pain (Singer et al., 2004), recent studies investigating neural responses using MVPA found that ACC and left AI activation were not specific to vicarious pain but instead reflects activation for firsthand and empathic affective unpleasantness such as disgust, while the right AI was activated only for empathic pain and disgust processing (Corradi-Dell'Acqua et al., 2016). Another study using MVPA suggested that the anatomically distinct mid-insula is bilaterally recruited for domain-general vicarious pain and not negative affective stimuli (Zhou et al., 2020). However, these findings contrast with an earlier MVPA study that found no evidence of AI and ACC activation in empathic pain processing compared to firsthand pain, with only mentalising regions active in empathic pain (Krishnan et al., 2016). The results of this study can be explained by methodological differences, since participants were explicitly instructed to imagine the pain depicted in an image happening to themselves, compared to the previous MVPA studies where participants were instructed to observe the stimuli, which would then engage mentalising networks involved in understanding the thoughts of others. Thus, the activity of the ACC and AI are strongly entangled in affect-sharing because both act in conjunction to generate the affect-sharing response.

Although not involved in affective processing, other cortical networks are recruited during affect-sharing depending on context. Mentalising regions such as the posterior superior temporal sulcus (pSTS), medial prefrontal cortex (mPFC), precuneus and temporoparietal junction (TPJ) are also recruited in affective empathic responding where socio-emotional context is not immediately available to the observer (Decety and Lamm, 2007; Decety and Sommerville, 2003; Masten et al., 2011; Morelli et al., 2014; Zaki et al., 2009). Specifically, the TPJ is involved in inferring transient mental states such as intentions, goals, and desires. In contrast, the mPFC is involved in the attribution and storage of enduring mental states, such as intentions and beliefs to the self and others, mentalising during the perception and evaluation of affective states, and self-referential processing (Budell et al., 2010; Mitchell, 2009; Mitchell et al., 2006; van Overwalle, 2009). Indeed, the

dorsal mPFC (dmPFC) and TPJ both activate as part of the vicarious pain response (Krishnan et al., 2016). The precuneus is responsible for contributing mental imagery to represent another person's perspective and in the cognitive evaluation of emotional changes (Schurz et al., 2014; Tabei, 2015), while the STS incorporates social and biological cues to generate a representation of another person's belief state (Gallagher and Frith, 2003; Hooker et al., 2010).

In complex social situations, components of the perspective-taking and affect-sharing networks may be activated simultaneously and contribute to the final behavioural response. A meta-analysis of fMRI studies investigating affect-sharing and mentalising found activation overlap in the bilateral inferior frontal gyrus (IFG) and ACC (Arioli et al., 2021), while a separate meta-analysis assessing neural region clustering for affect-sharing and mentalising revealed an intermediary cluster encompassing the insula, precuneus and mPFC that combined affective and cognitive processing (Schurz et al., 2021). Together, these meta-analyses indicate that in many real-world situations the distinction between perspective-taking and affect-sharing may often not be clear-cut, despite their anatomical and functional differences. Indeed, recent conceptual models of empathy highlight the interconnection between perspective-taking and affect-sharing and their contribution to prosocial behaviour (Fig. 1).

Although the neural substrates of affect-sharing for the pain or sadness of targets have been well-documented, affect-sharing for other emotional states, such as happiness, pleasure, and fear, have been the focus of more limited studies. Importantly, a Bayesian meta-analysis of emotional brain responses found that the experience of emotions such as happiness, disgust, fear, anger and sadness is characterised not by localised brain region activation but by differentiated co-activation of cortical networks and connections to sub-cortical regions (Wager et al., 2015). Therefore, affect-sharing for many emotional states might also

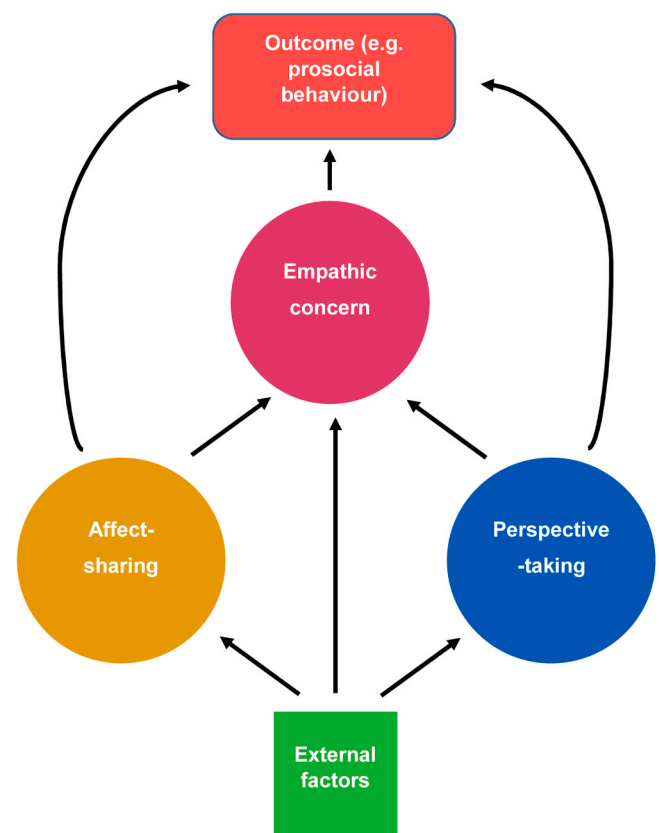


Fig. 1. Schematic model of empathy accounting for the role of external factors in affect-sharing, perspective-taking and empathic concern. Adapted from Vanman et al. (manuscript in preparation).

involve the activation of overlapping cortical networks. Consistent with this possibility, in one study that used conventional neuroimaging techniques to directly compare affect-sharing for pain, happiness and anxiety, affect-sharing for anxiety activated the pain matrix regions of the dACC and AI in addition to mentalising regions that included the dmPFC, precuneus and TPJ when compared to neutral images and affect-sharing for pain. Furthermore, affect-sharing for happiness activated the same mentalising regions of the dmPFC, precuneus and TPJ, and the ventromedial prefrontal cortex (vmPFC), which is associated with positive affect (Morelli et al., 2014). Because of the scarcity of affect-sharing studies that have investigated emotions other than pain or sadness, important questions remain in relation to which brain regions or networks are involved. However, the few studies that have been conducted do converge in highlighting the importance of the mentalising network in contributing to neural affect-sharing.

Affect-sharing is a complex phenomenon whereby the emotions of others do not automatically cause an empathic reaction that facilitates prosocial behaviour but rather that our response depends on a range of factors. These factors can be parsimoniously categorised into static physical cues, emotional cues, situational factors and the relationship between the observer and target (Table 1).

## 2. Static physical cues

When forming an initial impression of another person, static features that are physically apparent are first evaluated and influence subsequent affect-sharing. These static features can be broadly divided into *social category cues*, *humanness*, and *neoteny*.

### 2.1. Social category cues

Social category cues include the target’s sex/gender, age, race/ethnicity, attractiveness, socioeconomic status and trustworthiness. Observers implicitly use these cues to inform their evaluations of others, which then influences affect-sharing. Some social category cues such as sex/gender, age, social status, and attractiveness have been found to modulate affect-sharing (Jankowiak-Siuda et al., 2015; Olweus and Endresen, 1998; Stuijzand et al., 2016), but because empirical research on these are minimal, they will not be explored here.

#### 2.1.1. Race

In contrast to the limited research on age and gender, a considerable literature has focused on how target race influences affect-sharing. The data here have consistently identified an ingroup bias. When viewing African-American and White-American faces displaying pleasure and displeasure, African-American and White participants report subjectively stronger pleasure and displeasure, respectively, when the target’s race matches their own (Brown et al., 2006). Of central interest here are the neural mechanisms that underlie this response. Neuroimaging data reveals that relative to affect-sharing with the pain of racial outgroup members, affect-sharing with the pain of ingroup members is associated with greater activity in brain regions that play a crucial role in affective

**Table 1**  
External triggers and moderators of affect-sharing that have been documented in neuroimaging research.

Triggers/Elicitors		Moderators	
Static Physical Features	Emotional Cues	Situational Factors	Relationship Factors
Social category cues	Visual expressions	Modality of stimulus	Similarity to self
Race	Facial expressions	Sincerity	Friend vs. strangers
Trustworthiness	Crying (Tears)	Social status	Trust (including Reputation)
Humanness		Agency & Competition	
Neoteny			

processing, such as the dACC and AI. Moreover, greater activation in these brain regions has been linked to higher perceived pain ratings for ingroup relative to outgroup targets (Cao et al., 2015; Contreras-Huerta et al., 2013; Xu et al., 2009). Compared to affect-sharing for outgroup members, greater ingroup empathic bias for pain is associated with greater mPFC activation, a neural region involved in self-evaluative processing (Mathur et al., 2010).

One study examined how race might influence affect-sharing in participants from a country with a history of intense inter-racial conflict in South Africa (Fourie et al., 2017). The results showed that, for both Black and White participants, there was greater activation in affective processing regions such as the aMCC and AI when watching ingroup members experiencing physical pain compared to outgroup members. Racial effects also emerged when participants watched videos of social suffering sourced from the South African Truth and Reconciliation Commission. Relative to when outgroup members were the targets, viewing ingroup members in pain was associated with greater activation in core mentalising regions such as the precuneus, TPJ, dmPFC and pSTS, in addition to affective processing regions. These findings emerged despite both groups self-reporting no prejudice for racial outgroups, consistent with an implicit ingroup empathic bias (Fourie et al., 2017) and the systemic racism inherent to the participants’ broader social environment (Payne and Hannay, 2021). Together, these studies indicate that cognitive and affective processes are closely intertwined, with the former upregulating affect-sharing responses in a top-down manner for racial ingroup suffering.

However, it also seems likely that implicit racial attitudes outside conscious control may mediate the mechanisms involved in racial intergroup affect-sharing. A study found bilateral AI was activated more strongly for ingroup relative to outgroup pain, implicit racial ingroup bias predicted left AI activation for ingroup relative to outgroup pain (Azevedo et al., 2013). A meta-analysis of the neurobiological correlates of intergroup social cognition also supported a mediating role for implicit attitudes on racial intergroup affect-sharing. This revealed that affect-sharing for racial ingroup members activated the right dmPFC, right AI, and claustrum while affect-sharing for outgroup members activated the middle frontal gyrus (MFG; Merritt et al., 2021). This neural pattern appears consistent with the idea that affect-sharing with racial outgroup members is more cognitively effortful than affect-sharing with ingroup members.

Other studies have used event-related potential (ERP) measures to investigate the time course of racial empathic responding. Electrophysiological techniques such as electroencephalography (EEG) and ERP have a high temporal resolution that traditional neuroimaging techniques lack, allowing researchers to more clearly disambiguate explicit and implicit neural processes (Neumann and Westbury, 2011). One study found higher responses at the early N1 (110 ms) ERP component over fronto-central brain regions when White observers watched same-race faces in pain compared to Chinese faces, but no differential activity was found in later ERP components (Contreras-Huerta et al., 2014). In a separate study, heightened activity in the 280–340 ms time range (corresponding to the autonomic, affective component of affect-sharing) was observed in the IFG using source localisation analysis when White observers watched White facial expressions in pain but not Black faces in pain. However, no differences in parietal activity between same- and other-race pain were identified in the later 400–750 ms time window commonly attributed to cognitive evaluation and mentalising (Sessa et al., 2014). Also consistent with both of these studies, a later study showed that when White observers watched White hands in painful scenarios, there was a greater positive shift for amplitudes in the earlier 280–340 ms time window around frontal and central electrodes than for Black hands in pain (Fabi and Leuthold, 2018). These effects occurred independently of explicit attentional processes, and no significant relationship was found between later ERP activity and target race.

There are limited studies that have examined how target race affects



sensorimotor neural empathic responses to pain. In one influential study, transcranial magnetic stimulation (TMS) was used to manipulate sensorimotor neuron excitability by inducing electrical activity in the motor cortex region corresponding to a muscle close to the right index finger, while simultaneously measuring specified muscle activity. TMS was paired with images of Black and White targets experiencing painful stimulation to the same muscle as the observer. A significant reduction in corticospinal reactivity in the specified muscle – commonly observed in anticipation of self-experienced painful stimulation – was recorded when observing the same-race target. However, there was no change in muscle corticospinal excitability when viewing the other-race target in pain, despite a reduction in corticospinal reactivity present for unfamiliar violet targets. Additionally, corticospinal inhibition was negatively correlated with implicit racial ingroup preference. Such findings suggest that implicit prejudice and stereotyping play an important role in modulating sensorimotor empathic responses for other-race individuals via reductions in sensorimotor resonance caused by cognitive control processes, even if experience sharing for other-race pain is present overall (Avenanti et al., 2010).

Applying event-related desynchronisation (ERD) techniques to racial empathic bias to measure event-related decreases in sensorimotor potentials, another study found that the central beta ERD (13–30 Hz) band around the sensorimotor cortex was weaker when watching the pain of a racial outgroup member compared to a racial ingroup member (Riečanský et al., 2015). This indicates that racial empathic bias extends to empathic resonance on the sensorimotor level. This racial empathic bias may be due to perceived physical (dis)similarity that reduces TPJ activation to hinder the control of self- and other-perspective representations (Santiesteban et al., 2012), and thus decreases self-other overlap on the basis of motor resonance. This relationship between affect-sharing and similarity to self will be discussed further in Section 5.1.

Research on racial intergroup affect-sharing indicates that cognitive processes upregulate affect-sharing regions for racial ingroup members while sharing the emotions of racial outgroup members may be more cognitively effortful and do not readily activate affect-sharing regions. Time-course differences reveal that earlier-acting regions involved in affect-sharing regions activate for racial ingroup members but not outgroup members. At the same time, later-acting substrates for cognitive processing are not differentially affected.

### 2.1.2. Trustworthiness

Without additional social information, strangers are evaluated on trustworthiness from facial features assessed within a fraction of a second (Marzi et al., 2014; Todorov et al., 2011). One study examined whether affect-sharing is influenced by these rapid perceptions of trustworthiness at the neural level (Sessa and Meconi, 2015). The study reported greater ERP amplitude in the P3 (400–500 ms) time window in neural regions corresponding to the mentalising network when viewing trustworthy faces in pain compared to untrustworthy faces. It was suggested that reduced activation for untrustworthy faces might indicate that the neural circuitry involved in motivational avoidance behaviour is engaged when viewing untrustworthy faces, where a separate neuroimaging meta-analysis found that the right amygdala was activated in response to untrustworthy faces (Santos et al., 2016). In contrast, trustworthy faces trigger processing in the posterior cingulate cortex and medial frontal gyrus, which overlaps anatomically with the dmPFC (Santos et al., 2016), that elicits motivational approach behaviour. It was noted that trustworthy facial features might be used as a heuristic to judge desirable personality traits in the absence of social behaviour and assess whether they are worthy of affect-sharing (Sessa and Meconi, 2015).

In sum, the limited data on trustworthiness support the view that affect-sharing is modulated by social category cues in a top-down manner, with cues that signal a lower level of potential threat eliciting greater affective mentalising. For categorisation cues such as race, there

appears to be an initial affect-sharing bias against other-race targets (as reflected in reduced activation in regions such as the ACC, AI and mPFC), which is then mediated by later-acting cognitive processing that may either reduce the racial ingroup effect through explicit considerations not to appear racist or increase the racial ingroup bias when implicit prejudice is consciously acted upon. By contrast, mentalising brain regions for same-race targets appear to be more reliably activated and contribute more effectively to affect-sharing. Future research is now needed to measure functional connectivity in conjunction with real-time neural activation for affect-sharing based on social category cues, and to assess the effect of explicit attitudes on cognitive control of affect-sharing.

### 2.2. Humanness

The “humanness” of the target, and the degree to which they are genetically similar to humans, also appears to influence the magnitude of affect-sharing. In a study examining affect-sharing with the suffering of humans, primates, companion mammals (e.g., dogs, cats), utilitarian mammals (e.g., cows, pigs) and birds, skin conductance ratings (SCR) and self-reported affect-sharing ratings were higher for humans and species closer in phylogenetic similarity to humans (Westbury and Neumann, 2008). This result was replicated for still images of animals in distress, and affect-sharing ratings were lower for birds and reptiles than all mammals (Ingham et al., 2015).

Also supporting the idea that target ‘humanness’ is a determinant of affect-sharing, a recent study showed that watching pain applied to an adult human hand activated the right supramarginal gyrus (SMG) more than an equivalent degree of painful stimulation being applied to puppy and robot targets (Ionta et al., 2020). Participants also self-reported a higher degree of affective unpleasantness for the adult target’s pain than the puppy and robot targets. This was supported by a neuroimaging study which found less activation of the subcortical putamen for robots being abused than humans being abused (Rosenthal-von der Pütten et al., 2014). However, an ERP study investigating affect-sharing for the physical pain of humans and robots found larger P3 component amplitude for pain regardless of whether the target was a human or robot (Suzuki et al., 2015). However, it should be noted that there are a wide number of factors that may influence how human observers share the affect of robots (for review, see: Park and Whang, 2022), and which reflects an novel avenue of research in the domain of human-robot interactions.

The right SMG is a region anatomically proximate to the right TPJ involved in differentiating between the self and others that overcomes the emotional egocentricity bias by tagging and balancing the self and other perspectives (Bukowski et al., 2020; Lamm et al., 2016; Ruby and Decety, 2001, 2004; Silani et al., 2013; Tholen et al., 2020; Tomova et al., 2014). Integrating the function of the right SMG with affect-sharing, watching targets in pain leads to a tagging and balancing of the self- and other-perspective via right SMG activation to facilitate affect-sharing as a function of humanness, where this balancing of perspectives may not be possible if the target is not human.

There also appear to be important individual differences in how readily individuals spontaneously regard other non-human creatures and objects as like humans and thus share their experiences. Among observers that reported higher humanisation capacity, vegetables given human names and inflicted with painful stimuli elicited a higher P2 (130–180 ms) amplitude in the right centro-parietal EEG region relative to vegetables not given a human name, indicative of a stronger neural empathic response. Additionally, P3 (360–540 ms) activity is associated with mentalising (Sessa et al., 2014), and greater self-reported perspective-taking capacity has been shown to predict higher P3 amplitude at the right centro-parietal region for vegetables given names regardless of condition (Vaes et al., 2016).

Psychologically, greater empathy for vegetables that have been given names may reflect a perception of mind attribution that leads to the

understanding that the target has thoughts and feelings and is therefore entitled to moral rights (Waytz et al., 2010). Overall, these suggest that the cognitive neural regions that activate later in the empathic response modulate affect-sharing. Specifically, mentalising leads to target mind attribution, which then interacts with affective processing regions to modulate the degree to which observers share the emotions even of non-human targets.

### 2.3. Neoteny

Humans are evolutionarily motivated to provide care for children and infants (Glocker et al., 2009), and this has led to a perceptual bias to facilitate nurturing (i.e., the concept of *neoteny*), which corresponds to a set of infantile physical characteristics such as a large head, round face, small nose, big eyes, and more recessive chin that are perceived as cute, inducing positive affect and triggering attention, social approach and provision of care (Decety, 2021). The neotenous traits of a target modulate the degree to which the target is attributed with mental states and perceived as human-like, which then elicits an empathic response in the observer (Sherman and Haidt, 2011). This increase in affect-sharing for neotenous targets, which is discerned from visual, auditory and olfactory features of the target, may then act to expand the moral circle of the observer, whereby neotenous targets are judged to be worthy of moral consideration (Kringelbach et al., 2016). For this reason, neoteny may generate a heightened empathic response in human observers that also generalises to cute animals.

Several studies have documented this effect of neoteny on empathic concern, but not affect-sharing. In one study, self-reported ratings of empathic concern for human targets were higher for individuals with more infant-like faces and voices than for adult-like targets (Lishner et al., 2008) and the neoteny effect was also found for cute animal faces (Steinnes et al., 2019; Zickfeld et al., 2018). Additionally, heightened target vulnerability based on cuteness assessment can affect the affect-sharing response, with vignettes of cute targets such as children, dogs or puppies recovering from a broken leg, evoking stronger empathic concern in participants than for an adult in an identical scenario (Batson et al., 2005). Analogously, vignettes of children, dogs and puppies being mistreated elicits higher empathic concern and distress ratings than the suffering of an adult human in identical circumstances (Levin et al., 2017). However, the lack of research investigating the impact of neoteny on affect-sharing has to be addressed in future research.

Past neuroimaging studies have assessed how neotenous features are neurally processed, and of which one uncovered activation of the reward processing region of the nucleus accumbens when women looked at emotionally neutral babies with neotenous features (Glocker et al., 2009). One neuroimaging study specifically speaks to how cuteness might function as a modulating factor of neural affect-sharing. In this study, when watching a painful stimulus be applied to a baby's hand, there was greater SMG activation for pain applied to a baby hand than puppy and robot hands but no difference with adult hands and higher self-reported affective unpleasantness for the baby target. But this was accompanied by weaker ACC activation compared to stimulation of adult humans, puppies and robots (Ionta et al., 2020). This latter finding contradicts past empathy for pain studies that reported heightened ACC activation in response to others' pain. Increased SMG activation and reduced ACC activation may indicate that observers were able to tag and balance the self- and other-perspective to better feel the pain of the baby without ACC input. It is unclear if this study had enough power with a small sample size of 14, with recent fMRI studies investigating the ACC and associated neural regions enlisting samples of 30 or more participants (Krishnan et al., 2016; Wang et al., 2014), and even up to 252 (Zhou et al., 2020). Additionally, it may be that watching a baby inflicted with pain activated a different neural network involved in responding to other-person agency (see Section 4.4). Thus, this study may also be an outlier and additional studies are needed to investigate

the role of neotenic influences on neural affect-sharing.

## 3. Emotional cues

From as early as 1872, it has been recognised that the emotion displayed by the target might play an important role in determining any affect-sharing response in the observer (Spencer, 1872/2016). Target emotional features are particularly relevant for affect-sharing since interpersonal affective communication is just as dependent on the conveyance of emotion by a target as an observer's ability to read emotions. Emotions are expressed primarily using visual cues, this modality will be the focus here. Although emotions can also be expressed through verbal cues and act on neural affect-sharing regions (Kotz et al., 2013; Sachs et al., 2018; Tabei, 2015), no empirical studies have measured this association directly.

### 3.1. Visual expressions

#### 3.1.1. Facial expressions

In addition to facial expressions conveying emotion, recognition of facial affect plays an important role in affective empathic responding (Baron-Cohen, 2002; Shamay-Tsoory et al., 2009; Uzevovsky et al., 2012). Therefore, emotional expressivity through facial cues may increase observers' emotional recognition and facilitate affect-sharing. However, research on the neural substrates of affect-sharing for facial expressions has been scarce and failed to identify consistent results. In one study, emotional target facial expressions increased affect-sharing in observers, with increased ACC activation for neutral facial expressions paired with painful stimulation compared to painful expressions. However, ACC activation decreased, and the secondary somatosensory cortex was activated when a painful or happy expression was paired with painful or non-painful stimulation to the face. These findings suggest that viewing the pain of others in an emotional context reduces affective responding but increases sensory responding (Han et al., 2009). In a later study, exposing observers to an emotional facial expression before viewing painful hand stimulation led to activation of the right MCC and left AI regardless of emotion, but an angry expression paired with painful hand stimulation enhanced activation of the left dlPFC, which is involved in the cognitive reappraisal of affective information (Enzi et al., 2016). A meta-analysis of affective neuroimaging research found that happy faces activated the bilateral amygdala and reduced activation of the ACC in observers compared to negative emotions, where the insula was activated for disgusted and angry faces only (Fusar-Poli et al., 2009).

## 4. Situational factors

In addition to target physical and emotional features influencing affect-sharing at the neural level, situational factors and context can alter how targets and interpersonal contexts are perceived, further modifying the neural empathic response. Such situational features include stimulus modality, sincerity, social status, and intergroup competitions.

### 4.1. Modality of empathic stimulus

Observer affect-sharing appears to vary as a function of stimulus modality. A recent behavioural study showed that greater affect-sharing was elicited by emotional relative to physical suffering and that only affect-sharing with emotional suffering was associated with empathic concern (Stellar et al., 2019). In another study, empathy for physical pain was found to activate pain matrix regions, including the bilateral AI, aMCC and secondary somatosensory cortex, in a manner that generalised across vignette and audio-visual tasks (Jacoby et al., 2016). AI and aMCC co-activation during affect-sharing for physical pain was also identified in a meta-analysis that found a core affect-sharing

network comprising the left AI and left MCC was engaged across all affect-sharing tasks for pain and negative affect. However, empathy for pain additionally recruited the bilateral mid-insula and more extensive sections of the MCC compared to negative affect tasks (Timmers et al., 2018).

In the empathy for pain literature, differences in the neural activity elicited by facial pain expressions relative to acute pain inflictions on body parts have been identified. When observers view painful facial expressions, there is strong activation in regions associated with emotional information processing, such as the ACC and amygdala, as well as mentalising, including the mPFC and STS (Vachon-Preseau et al., 2012). Two separate meta-analyses investigating affect-sharing by stimulus modality found that, in addition to the core affect-sharing network, painful stimulation to a body part activated the IFG, inferior parietal lobule (IPL) and the dmPFC relative to observing painful expressions or cue-based signalling of pain stimulus (Lamm et al., 2011; Timmers et al., 2018). Also speaking to important differences between these two types of empathy-evoking stimuli, in a study that assessed the temporal dynamics of empathy-for-pain processing, face pain stimuli were found to be processed faster than body pain stimuli (Sun et al., 2017). Another recent study used inter-subject phase synchronisation to measure temporal and task-based variation in functional connectivity (Xu et al., 2020). The results showed that, relative to a non-painful image of a hand, acute pain infliction activated a network comprising the bilateral AI and MCC (thought to subserve vicarious pain processing) and a social cognitive network including the dmPFC, IFG, postcentral, and bilateral SMG (thought to modulate affect-sharing for a target's physical pain). However, no specific network was found for target painful expressions compared to non-painful facial expressions (Xu et al., 2020). These findings suggest that exposure to acute pain inflictions activates regions involved in encoding sensorimotor information and not emotional cue processing and may co-activate with mentalising regions to integrate sensorimotor information with information about the target's beliefs, thereby eliciting affect-sharing via an alternate neural pathway in situations where explicit affective information is not present.

An important qualifying factor that must be noted about the modality effects is that the differences in neural activation reported for each stimulus modality may be a result of the salience and explicit attention paid to the stimulus. One fMRI study using MVPA to investigate affect-sharing responses to images of targets' limbs that varied by pain presence, stimulus valence and emotional arousal and its overlap with firsthand experience of pain (Corradi-Dell'Acqua et al., 2011). This study found bilateral AI activation for firsthand pain and negatively valenced images regardless of pain presence while simultaneously revealing activation of the right middle insula and MCC for painful images regardless of valence, consistent with an anatomical and functional separation in the processing of pain and negative affect (Corradi-Dell'Acqua et al., 2011). However, it was later suggested that because the firsthand pain inflicted on the observer (noxious thermal stimulation only) in this study differed from the stimulus modalities of the presented images, a mismatch in modality might have resulted in limited activation of the firsthand pain regions. Furthermore, the higher salience of negative stimuli may have activated the bilateral AI rather than the aversive content of the stimuli (Valentini and Koch, 2012). In another fMRI study investigating firsthand and vicarious pain for a target where the observer's attention was directed towards a body part inflicted with pain, affective overlap between firsthand pain and affect-sharing for target pain was identified but there was no somatosensory sharing for the pain of others (Hartmann et al., 2021). Taken together, there is evidence that the modality of the empathy-eliciting stimulus causes differential neural activation across affective, mentalising and somatosensory regions, but that there are important inter-study differences relating to stimulus-matching and observer attention that make it difficult to compare results, and must be addressed in future research.

#### 4.2. Sincerity

Another situational factor that might influence affect-sharing involves the perception of whether targets are expressing the appropriate emotions in a given situation. In other words, whether there is perceived congruence between contextual cues and affective response. Highlighting the importance of perceived congruence, an ERP study investigated the time course of congruent and incongruent empathic activity. The results showed that activity in the fronto-central and parietal regions within the N2 and P3 time windows (250–360 ms) increased for painful expressions and acute pain infliction to an arm but not for acute pain infliction to a face with a neutral expression (Sun et al., 2017). In another study, a reduced belief in the targets' pain weakened observers' neural empathic response as indexed via lower P2 component (175–195 ms) amplitude in the fronto-central region. This was also related to subjective ratings of the targets' pain. A follow-up neuro-imaging study revealed heightened activation of the bilateral AI, post-central gyrus and IPFC in response to targets believed to be in genuine pain compared to those not believed to be in pain (Wu and Han, 2021). Together, these findings highlight the role of others' beliefs in the affect-sharing process, and specifically that neural networks associated with mentalising co-activate with and contribute to affect-sharing.

#### 4.3. Social status

Social status refers to the instrumental social value that another person is perceived to possess based on respect and prestige and is separate from socioeconomic status (Anderson et al., 2015). Only one study has tested the role of social status as a determinant of affect-sharing at the neural level and found evidence of differential empathic responses to social groups perceived as vulnerable versus groups perceived as 'deserving' of their lower status. The results revealed increased aMCC and AI activation for the pain of targets whom observers believed had acquired AIDS through blood transfusion relative to targets who contracted AIDS via intravenous drug use. Also consistent with the idea that top-down cognitive control, such as the consideration of explicit social attitudes, interacts with affective neural processes to modulate affect-sharing, a follow-up study showed that positive attitudes towards drug users were associated with greater mPFC activation (Decety et al., 2010).

#### 4.4. Agency & competition

Affect-sharing has also been shown to vary on the basis of the agency of others in inflicting pain on others and competition with other people, including against members of a non-racial outgroup. In situations where the agency and intentions are processed in conjunction with affect-sharing, regions that encode other-person agency or action intentionality are activated alongside affect-sharing and may make empathy-inducing stimuli more salient to the observer, and this includes stimuli that are perceived as a danger to the self. Consistent with this idea, one study found evidence for a differential affect-sharing response when observers viewed the bodily pain of a target caused accidentally by themselves relative to pain intentionally caused by another person (Akitsuki and Decety, 2009). In scenarios where another person was present in the frame, regions involved in processing social interaction such as the TPJ, IFG and mPFC were activated compared to trials with only one person in frame. In the other-caused pain group, there was heightened activation of the left IFG alongside pain processing regions of aMCC and insula and increased functional connectivity between the left amygdala and medial orbitofrontal cortex (mOFC) was detected. In contrast, for accident-caused pain there was stronger functional connectivity between the left amygdala and pain matrix regions only (Akitsuki and Decety, 2009). The left amygdala has been shown to respond to fearful events and detect danger (Phelps et al., 2001; Uematsu et al., 2012), and social threat has been shown to elicit



increased connectivity between the left amygdala and mOFC (Coccaro et al., 2007). According to Akitsuki and Decety (2009), while the perception of pain is viewed as a threat in both scenarios, target pain caused by another person is perceived as more salient due to the agency of the person causing harm to the target and, thus, as a greater danger than self-inflicted pain. Increased activation of IFG for other-inflicted pain also suggests that agency perception is integrated with social movement perception and attribution of pain meaning (Budell et al., 2010; Iacoboni, 2005; Vachon-Preseu et al., 2012).

Affect-sharing also varies based on group membership, which differs from racial empathic bias in the sense that membership of these groups is not physically evident to the observer and may not be known until the observer interacts with the target. This group affect-sharing effect operates on the basis that ingroup members typically elicit affect-sharing (Batson and Ahmad, 2009) and members of an outgroup are perceived to be directly competing against the ingroup in a zero-sum manner and thus elicit a reduction in affect-sharing (for review, see Cikara et al., 2011). One fMRI study investigated soccer fans' affect-sharing for targets who either supported the same team (ingroup) or supported a rival team (outgroup). The pain of outgroup members was rated less negatively than the pain of ingroup members and, when observers were given the option of receiving an electric shock so the target would not need to, opted to receive the shock to save an ingroup member more often than an outgroup member. Furthermore, watching the pain of ingroup members activated the left AI more strongly than the pain of outgroup members, with left AI activation also predicting taking the electric shock for the ingroup target but not for outgroup targets. Conversely, negative evaluations of outgroup targets predicted greater activation of the right nucleus accumbens (NAcc), a neural region associated with reward processing and deriving pleasure from the misfortunes of others, and predicted reduced helping behaviour for the outgroup target (Hein et al., 2010). In another fMRI study investigating affect-sharing for the pain of targets on the basis of ethnicity (Swiss descent vs. Balkan descent), there was stronger left AI activation for the pain of Swiss targets than Balkan targets (Hein et al., 2016).

Group membership effects on affective empathy have also been observed for arbitrary group membership. In a behavioural study where participants were randomly allocated into a 'team' then placed into competition with each other, observers felt more affect-sharing for the negative and positive situations of ingroup targets and unaffiliated targets compared to outgroup targets. This outgroup affect-sharing bias effect continued even after direct competition between groups ended (Cikara et al., 2014). Observing the emotional expressions of arbitrary ingroup members has been demonstrated to activate a network of brain regions purported to be the mirror neuron system, including the temporal poles, left insula, left IFG, MTG and inferior temporal gyrus, but it should be noted that this study did not explicitly ask observers to share the affect of the target (Krauthaim et al., 2019). Furthermore, when participants of different races were arbitrarily divided into separate groups and looked at painful and non-painful images of targets that varied by group and race, there was no effect of group membership in any ERP component and there was only an effect of target race in the fronto-central N1 (110 ms) component (Contreras-Huerta et al., 2014). This effect could be explained by a tendency towards competition with others, as high social dominance orientation (the tendency to believe in group-based hierarchies that is associated with a competitive worldview), has been shown to predict reduced affect-sharing for the negative emotions of outgroup targets on the basis of their race and arbitrary group (Hudson et al., 2019). Thus, the agency of others and perceived competition between groups may override affect-sharing for members of different groups, and minimal group membership may not be enough to overcome the modulatory changes in affect-sharing caused by membership of other groups.

## 5. Relationships

### 5.1. Similarity to self

The role of target similarity to the self in facilitating affect-sharing has been noted as early as the 18th century (Hume, 1739–1740/2007; Smith, 1790/1976). Evidence for this observation would be found in the 20th century, with psychological research finding that perceived similarity of the self and other fully mediating the association between empathic concern and willingness to help others (Cialdini et al., 1997). Self-other overlap has been observed neurally, with the right IFG and right PFC activated for self-awareness which are critical in processing self-other overlap (Decety and Sommerville, 2003). For affect-sharing, higher target similarity appears to increase affect-sharing and empathic concern via the mentalising network (Houston, 1990; Majdandžić et al., 2016; Nelson et al., 2003; Nelson and Baumgarte, 2004). Several behavioural studies have shown that, when presented with vignettes of targets experiencing negative emotions caused by dispositional self-attributes, observers who possessed similar attributes to the target reported higher empathic concern for that target than those who did not share those attributes (Houston, 1990; Nelson et al., 2003). In another study, when given vignettes of targets experiencing distress from cultural attitudes, American observers reported less affect-sharing with distress reflecting a dissimilar cultural perspective than distress from a similar cultural perspective. This reduction in empathic concern was mediated by self-reported perspective-taking (Nelson and Baumgarte, 2004). Mitchell et al. (2006) used fMRI to reveal that activation of the vmPFC was stronger when an observer mentalised about a target with similar beliefs to themselves, relative to when they mentalised about a target with dissimilar beliefs. By contrast, mentalising with dissimilar targets more strongly activated the dmPFC. These findings suggest that perceived similarity to self plays a role in perspective-taking in a manner that is dissociable at the neural level.

In an fMRI study that manipulated the similarity of the targets' mental states to the observer before inflicting the target with pain, the left ventrolateral prefrontal cortex (vlPFC) was more strongly activated when mentalising with dissimilar targets and was negatively related to self-reported affect-sharing (Majdandžić et al., 2016). Additionally, the medial dmPFC, involved in generating representations from uncertain information (Mitchell, 2009), was associated with greater affect-sharing with dissimilar targets in the bilateral AI. Given the role of the vlPFC in self-perspective inhibition, particularly when reasoning about others' mental states (Hartwright et al., 2012), these data suggest that the vlPFC and medial dmPFC activate concurrently to suppress the self-perspective and generate representations of a dissimilar target's mental state that contribute to greater affect-sharing.

When accounting for the role of self-other overlap (the degree of overlap between cognitive representations of the self and others) and the activation of the mPFC and ACC in both self- and close-other referential thought (Aron et al., 1991; Wang et al., 2012; Zhu et al., 2007), it has been suggested that the degree of target similarity to self might also modulate the empathic response via aMCC or mentalising network activity. Consistent with this idea, one study investigating the neural substrate of affect-sharing for similarity found greater aMCC activation when observing the self's facial expressions in pain compared to others (Benuzzi et al., 2018).

Importantly though, similarity to self is not static and can be manipulated. An intervention of perceived intergroup connectivity in a study investigating affect-sharing for members of arbitrarily designated groups revealed that reductions in affect-sharing for the emotions of outgroup targets relative to ingroup targets did not disappear entirely, but were greatly ameliorated in the integrated intervention compared to the segregated condition (Cikara et al., 2014). In one recent study, event-related desynchronization (ERD) techniques were used to investigate event-related suppression of EEG oscillatory activity when watching painful stimulation be applied to a target hand that was



visually overlapped with the observer's hand. The results revealed that there was stronger suppression of activity in the mu (7–12 Hz) and beta (13–30 Hz) ERD bands over the sensorimotor cortex compared to when target pain was not overlapped with the observer. This self-other overlap effect was amplified for observers who reported higher bodily self-attribution of the target hand (Riećanský et al., 2020). Moreover, in an ERD experiment of white Finnish participants, racial differences were reduced by transferring people to black-skinned avatars in virtual reality before watching a painful stimulus be applied to a black hand. Despite empathic racial bias remaining intact on behavioural measures, amplified beta ERD in sensorimotor sites was recorded in anticipation of and during painful stimulation of a black target's hand when the observer was transferred to a black body compared to observing from a white body (Harjunen et al., 2022). Combined with prior ERD research on empathic racial bias (Riećanský et al., 2015), these studies indicate that greater sensorimotor empathic pain resonance can be elicited when observers' perceived similarity to the target is increased.

### 5.2. Friend vs. stranger

Another potentially important determinant of one's empathic response to another is social closeness, or whether the target is someone with whom an interpersonal relationship has been established, or a stranger. This friend effect of affect-sharing has been documented in psychological research, with people feeling more empathic concern and engaging in more helping behaviour for family and friends than strangers (Cialdini et al., 1997). However, neural evidence is somewhat mixed as to the precise nature of these effects. While one study found evidence of affect-sharing for positive (but not negative) emotions via self-report and the later P3 component when watching friends but not strangers benefit in an emotional gambling task, another study found that for negative emotions affect-sharing occurred regardless of familiarity (Motomura et al., 2015).

Leng and Zhou (2010) also identified a higher amplitude of the later latency P3 ERP component when observers watched friends win or lose in a monetary gambling task compared to strangers, but no differences in early neural activity between friends and strangers. However, another study primed participants with photographs of strangers or friends before presenting painful hand stimulation and happiness-related hand images (hand on top of money). In this study, the early N110 (80–150 ms) component was found to be less negative, and the late positive potential (LPP; 400–800 ms) component more positive when watching the friend (relative to the stranger) in pain. By contrast, in the empathy for happiness task, there was no early effect between friends and strangers, but the friend prime elicited larger N250 (200–300 ms), smaller P300 (300–400 ms) and smaller LPP amplitudes for friends compared to strangers (Wang et al., 2016). As noted earlier, heightened N110 responses are associated with early pain processing, increased P300 responses are associated with top-down cognitive modulation of neural regions involved in affect-sharing (Fan and Han, 2008), and the N250 component is sensitive to emotion regulation (Lamm and Lewis, 2010). Wang et al. (2016)'s study therefore provides evidence for top-down control in affect-sharing based on relationship, with later-acting cognitive regions activating for friends that may be due to salience, emotion regulation or reduction in cognitive effort.

It has also been shown that, for unfamiliar, de-identified targets, pain for social exclusion activates mentalising neural regions such as the mPFC, dmPFC and precuneus, with affective pain processing regions such as the dACC and AI only active in observers with high trait affect-sharing (Masten et al., 2011; Meyer et al., 2013). However, in observers watching the social rejection of a friend relative to a stranger, activation is heightened in pain matrix regions such as the dACC (Beeney et al., 2011), in addition to regions associated with firsthand experience of social exclusion such as the AI, and regions involved in self-processing, such as the mPFC (Meyer et al., 2013). Interestingly, Meyer et al. (2013) also identified an association between self-other overlap and activation

of the dACC and AI when watching the social pain of friends, with increased functional connectivity between mPFC and affective pain regions when witnessing a friend's social pain. Additionally, the self-reported emotional closeness between the target and observer was correlated with bilateral AI and dACC activation for a friend's social exclusion, with the relationship between empathy for social pain and emotional closeness mediated by IFG activation (Beeney et al., 2011). In the event of a romantic relationship, imagining a loved one in physical pain was associated with greater activity in the insula and ACC, greater overlap between self and other, as well as less activity in the right TPJ relative to perceiving the pain of a stranger (Cheng et al., 2010). These findings suggest that top-down cognitive control increases the strength of the affect-sharing response to the emotion or pain of friends, which is potentially first aroused by bottom-up socio-affective resonance.

Taken together, although the precise nature of these effects has been shown to vary, most prior research suggests that social closeness increases affect-sharing via more strongly activating affect-sharing regions such as the dACC and AI and facilitated by later-acting mentalising regions such as mPFC and decreased activity in the TPJ. Further work is needed to determine the precise networks underlying increased affect-sharing for socially close targets, the temporal components of this activity and its connection to self-other overlap.

### 5.3. Trust

Because interpersonal relationships largely depend on trust (Reis et al., 2000), this may also be an important determinant of affect-sharing. In addition to perceived trustworthiness judged on physical characteristics, trust history between observer and target, as well as the appraisal of others' social behaviour, may influence when and how strongly affect-sharing is elicited.

One fMRI study measured empathy for the pain of fair and unfair players as determined by an economic game conducted before the affect-sharing task – with unfair players labelled as untrustworthy. Observers exhibited reduced activation in affect-sharing-related brain regions, including the ACC, AI, and fronto-insular cortex, as well as increased activation in the reward-processing nucleus accumbens, when viewing the pain of unfair relative to fair players, with each of these effects particularly evident in men (Singer et al., 2006).

Greater passive intergroup contact has been argued to increase trust for outgroup members and subsequently facilitate greater affect-sharing with the outgroup, and this has shown in countries with a history of intense inter-ethnic violence (Malhotra and Liyanage, 2005; Shani and Boehnke, 2017). Two studies have investigated the impact of intergroup trust on empathic neural responding through passive contact with outgroup members. The first study focused on Chinese minorities raised in Western countries, and found no difference in neural affect-sharing between same-race and other-race pain, with similarly heightened ACC and AI activity in response to the pain of both groups (Zuo and Han, 2013). The second study similarly showed that, among Chinese university students studying in Australia, greater contact with White people during adulthood increased ACC activation to similar levels as same-race pain when viewing the pain of White targets regardless of the closeness of contact (Cao et al., 2015).

One specific subset of trust relates to the reputation of a target. Reputation refers to the judgement of character as evaluated by others, which is important in altruistic interaction (Izuma, 2012) and may inform assessments of target trustworthiness. Few neuroimaging studies have explicitly assessed how reputation impacts neural affect-sharing. However, in one study, participants were shown videos of targets playing the repeated prisoner's dilemma game where targets either cooperated with others more than they betrayed them (good reputation) or betrayed more than they cooperated (bad reputation). They were then asked to watch those targets have painful or non-painful stimulation applied to their finger. The results showed that watching good reputation targets in pain activated the left AI and left IFG more relative to

watching bad reputation targets in pain, indicating that observers had greater neural affect-sharing with targets of good reputation and less affect-sharing with bad reputation targets (Zheng et al., 2016).

In another study, Jewish participants showed higher activation in the ACC, MTG and reward-processing region of the striatum, in addition to greater functional connectivity of the right AI and right mPFC with the left ACC, when watching the pain of anti-Semitic neo-Nazi targets relative to non-hated targets (Fox et al., 2013). As the MTG and mPFC are involved in emotion regulation and cognitive reappraisal, these results suggest that functional networks associated with pain and cognitive reappraisal are co-activated in response to the pain of hated targets. However, the findings contradict a study that found reduced ACC activation in response to unfair players' pain (Singer et al., 2006), and may be due to the many functional outputs that the ACC is involved in, including conflict monitoring (Greene et al., 2004), threat detection and fear (Jhang et al., 2018), emotional salience (Duggirala et al., 2022) and affective unpleasantness (Corradi-Dell'Acqua et al., 2016). Indeed, Fox et al. (2013) interpret their findings of heightened ACC activation for the pain of neo-Nazi targets to be associated with increased salience of the target's pain and be indicative of context-related attention processing of the pain of hated targets.

How the reputation of a target influences affect-sharing has been shown to be malleable. A neuroimaging study investigated how the judgement of character for a member of an outgroup generalised to the outgroup as a whole. Here, observers expected to receive painful shocks but were informed that a member of an ingroup (Swiss person) or outgroup (Balkan person) forfeited money to stop the pain being inflicted on the observer, then saw a different ingroup or outgroup member be inflicted with pain (Hein et al., 2016). After intervention from an outgroup member, there was increased activation in the left AI when viewing pain of outgroup members compared to before the intervention, and compared to receiving an ingroup intervention, consistent with increased affect-sharing for the outgroup member.

Finally, in an ERP experiment where people were primed with morality labels and then shown painful and non-painful hand stimulation, the N2 (240–290 ms) amplitude was more negative in response to the pain of good targets compared to bad targets, suggesting a reduction in the early affective component of the affect-sharing response for targets judged as immoral (Cui et al., 2016). In addition, standardized low-resolution brain electromagnetic tomography also revealed greater activation in the vmPFC, a region that relates to integrating mental state knowledge of targets with affective information (Benoit et al., 2014; Winecoff et al., 2013).

Taken together, current literature provides evidence for enhanced affect-sharing for trustworthy people, including targets with good reputations, and out-group members for whom there has been greater intergroup contact, and these effects may at least partially reflect greater mentalising for the target. However, because in many of these studies trust was not directly measured but only inferred, future research is now needed that directly measure trust to provide a stronger test of when, why and how trust influences affect-sharing, and how these effects present at the neural level.

## 6. An integrative model of external factors and affect-sharing

The external factors described in this paper can be broadly categorised into factors that promote competition or cooperation, and factors that signal similarity to self. Firstly, competition/cooperation factors include race, in-/out-group membership and the trustworthiness of targets and may motivate observers to engage in or to avoid affect-sharing with the target (Zaki, 2014). The competition component of these factors are associated with an evolutionary motive to compete against others, ostensibly for finite resources, that reduces affect-sharing for those targets (Cikara et al., 2011). Under different circumstances, these same external factors may engender cooperation, which is also proposed to have evolved in humans (Apicella and Silk, 2019) and

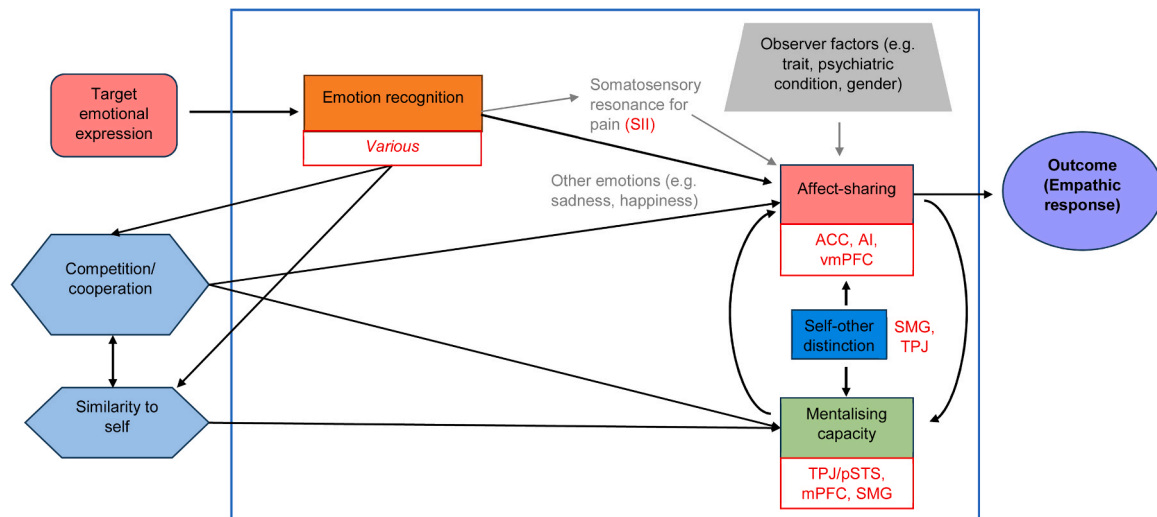
include target trustworthiness, racial or non-racial ingroup members and whether the target is a friend, or affiliation with targets, as in the case of neotenous targets or romantic partners. For targets that observers wish to cooperate or affiliate with, observers will be motivated to engage in affect-sharing and thus produce an enhanced affect-sharing response.

Secondly are factors that modulate perceived similarity to self, which include whether the target is a friend or stranger or social categorisation based on physical cues or group membership. The existence of this system is related to the overlap between mentalising and similarity to self, as it is easier to understand the mental states of people that we are friends with, or of targets who share characteristics that make it less cognitively difficult to infer their mental states.

However, it is important to note that competition/cooperation and similarity to self are not mutually exclusive. For example, when observing the race of a target, the perceived similarity to self based on skin colour may be used as a heuristic by the observer that is interpreted as a signal to cooperate with the target or compete with them. Additionally, a field study of pastoral ethnic groups in Kenya found that intergroup cultural similarity predicted intergroup cooperation (Handley and Mathew, 2020), indicating an evolutionary connection between competition/cooperation and similarity to self. However, because competition/cooperation is associated with resources, which may either be material or psychological, and similarity to self being related to a base understanding of the mental states of others, these two grouping factors have been separated from each other.

We propose an integrative model of the modulatory effects of external factors on neural affect-sharing (Fig. 2). At the beginning of the process, before any affect-sharing can occur, the target must express some emotion or have visible pain inflicted on them. This emotion is then processed by the observer where, in neurotypical conditions, the emotion is recognised and processed in parallel by a series of neural networks on the basis of emotional valence and intensity (Nummenmaa et al., 2012). In the limited scenarios where observers are watching isolated emotional expressions or pain infliction devoid of context, this is processed directly by affect-sharing regions in the ACC, AI and, for positive emotions, the vmPFC (although for pain there is additional somatosensory resonance that is processed by the secondary somatosensory cortex). In most naturalistic scenarios, information about the emotion of the target is integrated with competition/cooperation information of the target and their perceived similarity to the observer, which may interact. The competition/cooperation social cognitive complex, which are underpinned by different brain networks where cooperation is processed by the mOFC and competition by the inferior parietal cortex and mPFC (Decety et al., 2004), delivers information directly to the affect-sharing system and mentalising system. The mentalising system is involved in understanding the mental states of targets and is underpinned by the TPJ and anatomically proximate pSTS, mPFC and SMG. There is a feedback loop between the affect-sharing system and the mentalising system, in such a way that understanding the mental states of a target informs whether an observer resonates with the emotions of a target, and affect-sharing for a target can inform their understanding of a target's mental states as identified in previous models of affect-sharing (Bird and Viding, 2014). The similarity to self system only sends information to the mentalising system, as there is evidence that higher mental state similarity between the observer and target increased affect-sharing via dmPFC activation but no evidence that higher similarity to self directly increased affect-sharing (Majdandžić et al., 2016).

At the same time, affect-sharing and the capacity to mentalise with others is underpinned by self-other distinction and the capacity to switch between self- and other-perspectives in the TPJ (Decety and Lamm, 2007; Santiesteban et al., 2012) and anatomically proximate SMG (Bukowski et al., 2020). Behavioural research has indicated that undermining self-concept clarity reduced affect-sharing for targets via self-other merging (Krol and Bartz, 2021), pointing to a critical role of self-other distinction in neural affect-sharing. Additionally, observer traits such as gender and mental health also influence neural



**Fig. 2.** Schematic diagram of the integrative model of external factor contributions to affect-sharing, their interaction with mentalising and associated neural regions. The light blue box represents internal observer processes, and hexagonal boxes indicate external factor umbrella categories. Brain regions are given in red text. Abbreviations: ACC = anterior cingulate cortex, AI = anterior insula, mPFC = medial prefrontal cortex, pSTS = posterior superior temporal sulcus, SMG = supramarginal gyrus, TPJ = temporoparietal junction, vmPFC = ventromedial prefrontal cortex.

affect-sharing, but an in-depth analysis of observer traits on affect-sharing are outside the scope of this paper (see Section 7.1 for a discussion of select observer traits). The contribution of these emotion processing, external factor processing and mentalising systems into affect-sharing and the production an emotional state in the observer (or lack thereof) would then lead to a behavioural outcome, such as prosocial behaviour directed towards the target or avoidance of a target that the observer does not trust.

## 7. Limitations and future directions

This review provides not only an overview of the progress in our understanding of external factors' role in affect-sharing but also an integrated model of affect-sharing and external factors and roadmap for future research in this area by identifying key gaps in this literature. Firstly, most affect-sharing studies contributing to this review focused on isolated cues and/or specific neural networks. Thus, although in any assessment of empathy the limitations of artificial stimulus cues such as decontextualised facial expressions are now well understood (for commentary, see Henry et al., 2023; Zaki and Ochsner, 2012), many studies continue to rely on such stimuli. This practice narrows our understanding of affect-sharing at the neural level, such as how affect-sharing interacts with other socio-cognitive processes, such as mentalising, to produce affect-sharing in naturalistic settings. Only a handful of studies have assessed how affect-sharing and mentalising interact at a neural level in settings where target race or situational context vary (Masten et al., 2011; Morelli et al., 2014; Zaki et al., 2009) or used sophisticated neuroimaging techniques to detect neural affect-sharing pattern activation in response to painful stimuli (Corradi-Dell'Acqua et al., 2016; Krishnan et al., 2016; Zhou et al., 2020). Further research is needed to incorporate naturalistic empathy-eliciting stimuli and more precise neuroimaging techniques to move towards a more holistic understanding of affect-sharing. For example, applying the novel analysis technique of intersubject synchrony in fMRI to investigate stimulus-driven changes in brain activation and connectivity across participants has been applied to the processing of emotions to derive more sophisticated understandings of the neural regions involved (Nummenmaa et al., 2012; Sachs et al., 2020; Trost et al., 2015). Such techniques can be applied to external factor processing of neural affect-sharing.

Another important limitation in the current literature review is that it dominated by affect-sharing for one specific emotion, specifically,

empathy for pain or negative affect (e.g. sadness), without considering affect-sharing for other emotions. Due to the motivational nature of affect-sharing, divergent behavioural responses are expected between affect-sharing for positive and negative emotions (Zaki, 2014), and there is evidence that affect-sharing for positive and negative affect differs at the neural network level (Lamm et al., 2015; Morelli et al., 2014). Future research is now needed to explore the specific factors that elicit neural similarities vs differences in affect-sharing for positive and negative affect, including for social emotions such as guilt, and how affect-sharing may vary by other affective visual expressions such as tears (Hendriks et al., 2008) and emotional expression modalities such as auditory cues (Sachs et al., 2018).

Finally, greater attention should be paid to genetic and environmental factors that can modulate observer trait affect-sharing and how this might make certain external factors more or less salient to the observer (Abramson et al., 2020). In addition to external factors, these factors should also be considered when investigating how and when affect-sharing is elicited. This is especially the case with individual differences in dispositional affect-sharing and how it interacts with state affect-sharing in response to various external factors.

### 7.1. Observer factor interactions with external factors

A natural direction for the future research of external factor contributors to neural affect-sharing is to investigate its interactions with observer factors. Various observer factors have been noted in the literature to influence neural affect-sharing, which may then interact with external factors such as age, hormone levels, and clinical disorders such as depression.

An fMRI study investigating age-related differences in neural affect-sharing for pleasant and unpleasant touch found lower bilateral AI activation in older compared to younger women (Riva et al., 2018). Another related study investigating young, middle-aged and older men reported smaller age-related reductions in the right AI and aMCC activation for the pain of targets which was associated with declining trait affect-sharing (Chen et al., 2014). However, a large cross-sectional sample measuring self-reported trait affect-sharing found an inverted-u shaped association for women that peaked in middle age and decreased through old age, and a positive association between trait affect-sharing and age in men (Sommerlad et al., 2021). These conflicting results indicate that more research is needed to understand the

relationship between neural affect-sharing and observer age, as well as how observer age interacts with external factors to influence neural affect-sharing (Richter and Kunzmann, 2011).

A potential role for hormones in modulating observer affect-sharing has also been suggested. One hormone that facilitates behaviours that can lead observers to the acquisition and maintenance of social status is testosterone (Dreher et al., 2016; Eisenegger et al., 2011). Exogenous administration of testosterone in women has been shown to reduce their mentalising capacity, with this effect particularly pronounced for observers with low second-to-fourth finger digit ratios, a proxy for high foetal testosterone (van Honk et al., 2011). Exogenous testosterone administration in women also reduced mimicry of target emotional expressions, a proxy of affect-sharing (Hermans et al., 2006). A neuroimaging study investigating mentalising after testosterone administration in women found that, relative to a placebo condition, there was evidence of reduced connectivity between the left IFG and the bilateral SMG and ACC, a network involved in integration of sensory information with emotional states, when recognising and understanding the emotions of a target (Bos et al., 2016). Additionally, a separate neuroimaging study assessing affect-sharing for target pain and testosterone administration in women revealed no effect of testosterone on affect-sharing for pain (Heany et al., 2020). However, a more recent neuroimaging study using videos of targets describing negative events found no effect of testosterone administration on neural affect-sharing or mentalising activation (Puiu et al., 2022). Taken together, these studies indicate affect-sharing is not affected by testosterone but that mentalising with the thoughts and emotions of targets can be, albeit in a task-dependent manner. Future research is now needed to systematically investigate testosterone administration interactions with external factors such as target social status in a task-specific manner.

There are also some clinical conditions that are characterised by abnormal empathy, and specifically characterised by reduced affect-sharing for targets. For example, autism spectrum disorder appears to be characterised by a reduced mentalising capacity that has been linked to reduced mPFC activation but intact or even enhanced affect-sharing for targets linked to left AI activation (Bird et al., 2010; Dziobek et al., 2008; Fan et al., 2014). Conversely, psychopathy is associated with intact mentalising ability for the thoughts of targets but impaired spontaneous affect-sharing linked to reduced left AI and ACC activation (Berluti et al., 2020; Lockwood et al., 2013; Meffert et al., 2013). Alexithymia also often occurs alongside some mental health conditions, and presents as difficulties identifying and describing emotions in the self. Higher levels of alexithymia is associated with reduced left AI activation in response to a target's emotions (Bird et al., 2010) and has been linked to impaired perceptual switching in the IFG and reduced self-other distinction (Saito et al., 2016; Tei et al., 2023). Because affect-sharing appears to be processed differently, external factors may interact uniquely with psychopathy, autism spectrum disorder or alexithymia to produce divergent affect-sharing responses. For example, difficulties in understanding social context for people with autism spectrum disorder may lessen the impact of other-person agency, and difficulties in self-other switching may lead to reduced affect-sharing in the AI and ACC in situations where targets are similar to the observer for people with alexithymia. For this reason, future research should investigate the influence of external factors on neural affect-sharing in people with empathic conditions.

## 8. Conclusion

Considering the role of affect-sharing in motivating and promoting prosocial behaviour (Cialdini et al., 1997; de Vignemont and Singer, 2006; Lamm et al., 2019; Masten et al., 2011), it is of critical importance to develop a better understanding of how external factors influence affect-sharing on the behavioural and neural level to facilitate greater societal cohesion. Here, in service of this goal, we provide the first integrated review of studies across social, affective and cognitive

neuroscience focused on how external factors influence neural affect-sharing. This research literature reveals many factors that modulate affect-sharing and shows how these are underpinned by dynamic activation of associated brain regions. Targets with vulnerable, trustworthy, and emotionally expressive features elicit greater activation in regions linked to affect-sharing, such as the AI, ACC and IFG. In circumstances where explicit situational factors such as social status, stimulus modality, social closeness and interpersonal trust provide additional context to the target's emotions, top-down cognitive processing plays an active role in modulating affect-sharing. Specifically, this may occur through the co-activation of neural networks involved in mentalising and affect-sharing in response to similar or trusted targets to enhance affect-sharing or through activation of mentalising regions in the absence of affect-sharing activity to compensate for a lack of affective resonance such as for other-race targets or untrustworthy targets. Future research is now needed using more ecologically valid paradigms to gain deeper insights into when, how and why specific external factors influence affect-sharing, as well as how these different factors might themselves interact.

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