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Issue: *Social Neuroscience: Gene, Environment, Brain, Body***The neuroevolution of empathy**

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There is strong evidence that empathy has deep evolutionary, biochemical, and neurological underpinnings. Even the most advanced forms of empathy in humans are built on more basic forms and remain connected to core mechanisms associated with affective communication, social attachment, and parental care. Social neuroscience has begun to examine the neurobiological mechanisms that instantiate empathy, especially in response to signals of distress and pain, and how certain dispositional and contextual moderators modulate its experience. Functional neuroimaging studies document a circuit that responds to the perception of others' distress. Activation of this circuit reflects an aversive response in the observer, and this information may act as a trigger to inhibit aggression or prompt motivation to help. Moreover, empathy in humans is assisted by other domain-general high-level cognitive abilities, such as executive functions, mentalizing, and language, which expand the range of behaviors that can be driven by empathy.

**Keywords:** evolution; affective neuroscience; social neuroscience; empathy

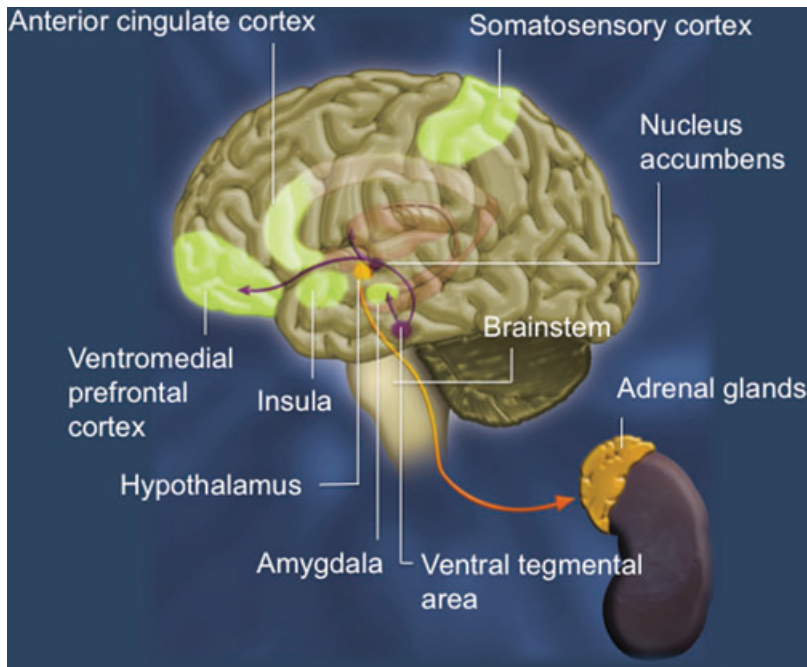
**Introduction**

The experience of empathy is a powerful interpersonal phenomenon and a necessary means of everyday social communication. It facilitates parental care of offspring. It enables us to live in groups and to socialize. It paves the way for the development of moral reasoning and motivates prosocial altruistic behavior.

The term *empathy* is applied to various phenomena that cover a broad spectrum, ranging from feelings of concern for other people, experiencing emotions that match another individual's emotions, knowing what another is thinking or feeling, to blurring the line between self and other.<sup>1,2</sup> This conceptual diversity explains the difficulties in measuring empathy. None of the attempts to quantify it with self-reports, peer ratings, or rating scales of observed behavior have been able to capture the entire range of affective, cognitive, and behavioral components of empathy. Moreover, one crucial and distinctive feature of human empathy is that it is not restricted to interaction with kin, nor does it have to be prompted by the actual perception of distress signal or emotion contagion. Rather,

it can be extended to strangers and even members of different species and generated from cognitive processing, like imagination and conscious rationalization.

Given the complexity of what the phenomenological experience of empathy encompasses, investigation of its neurobiological underpinnings would be worthless without breaking down this construct into component processes.<sup>3,4</sup> Molar constructs developed by social scientists provide a useful means of understanding highly complex activity and mental functioning without needing to specify each individual action or process by its simplest components, thereby providing an efficient approach to describing complex system.<sup>5</sup> Yet, it does not follow that the organization of psychological phenomena maps in a 1:1 fashion into the organization of the underlying neural substrate. In reality, empathy, like other social processes, draws on a large array of brain structures and systems that are not limited to the cortex, but also include the brainstem, the autonomic nervous system (ANS), hypothalamic–pituitary–adrenal axis (HPA), and endocrine systems that regulate attachment and social affiliation,



**Figure 1.** Converging evidence from animal research, functional imaging studies in normal individuals, and lesion studies in neurological patients shows that empathy draws on a large array of neurobiological systems that are not limited to the cortex (insula, anterior cingulate cortex, and orbitofrontal cortex), but also the midbrain (e.g., periaqueductal gray) and brainstem, and includes the autonomic nervous system (ANS), HPA axis, and endocrine systems that regulate bodily states, emotion, and reactivity. Caring for others draws on general mammalian neural systems of reward and social attachment. Moreover, empathy is not unique to humans, as many of the biological mechanisms are shared with other mammalian species. However, humans are special in the sense that high-level cognitive abilities, such as executive function, language, and mentalizing, implemented by the prefrontal cortex, are layered on top of phylogenetically older social and emotional capacities. These evolutionarily newer aspects of information processing expand the range of behaviors that can be driven by empathy, and expand flexibility like caring for and helping outgroup members or even individuals from different species.

bodily states, emotion regulation, and reactivity (Fig. 1).

This paper examines how empathy has evolved in the context of parental care in mammalian species and what neurobiological mechanisms underlie its operation. With continuing maturation of the prefrontal cortex, development of a sense of self, and more complex forms of cognitive abilities such as mentalizing and language, humans exhibit more advanced and flexible levels of empathy tied to perspective taking. This results in greater understanding of other's affective and mental states, but it does not guarantee that the outcome is benevolent. After all, it is not adaptive to extend one's empathic concern to all. Moreover, various situational and interpersonal variables influence the processes involved in empathy, and these effects occur at different levels of neurobiological organization.

## Evolutionary origins of empathy

The human social brain, as well as all other mammalian brains, is fundamentally built upon ancient emotional and motivational value systems that generate affective states as indicators of potential fitness trajectories. While one needs to be cautious regarding the forms of behaviors in the animal kingdom that have been interpreted as evidence of empathy,<sup>6</sup> basic affective states—and the neural mechanisms to support them—are homologous in all mammals.<sup>7</sup> Over millions of years of evolution, efficient and manifold neurobiological mechanisms have evolved for differentiating hostile from hospitable stimuli and for organizing adaptive responses to these stimuli.<sup>8</sup> This integrated set of neural systems is genetically hardwired to enable animals to evaluate and respond unconditionally and readily to threatening

or nurturing, unpleasant or pleasant, and appetitive or aversive stimuli by using specific response patterns that are most adaptive to the particular species and environmental condition. The architecture of this affect system maps onto the neural circuitry of the limbic system, which includes the hypothalamus, the parahippocampal cortex, amygdala, and several interconnected areas (septum, basal ganglia, nucleus accumbens, anterior insular cortex [AIC], and retrosplenial cingulate cortex) and underlies rapid and prioritized processing of affective signals. The limbic regions also project to the orbitofrontal cortex (OFC) and anterior cingulate cortex (ACC), which are involved in the evaluation and regulation of emotion, as well as decision making. Moreover, aversive and appetitive stimuli are processed by partially independent neural circuitry with distinct subregions of the OFC and striatum.<sup>9</sup> The functional separability between positivity and negativity is also supported by the opposing roles for dopamine and acetylcholine in the striatum in the control of GABA output systems for approach and avoidance.<sup>10</sup>

Basic affective circuits emerged much earlier in brain evolution than higher cognitive capacities. Social species care for offspring sufficiently long so that they too can reproduce. As such, the genetic legacy of a species is associated with the ability to perceive and respond to emotional expressions of hunger, pain, distress, or fear. Such signals are primary and powerful stimuli that call for parental care. At the behavioral level, it is apparent from the descriptions of ethologists that behaviors homologous to empathy and sympathetic concern can be observed in other mammalian species. Without doubt, some aspects of empathy are present in other species, such as emotion contagion and concern.<sup>11</sup> For example, mother vervet monkeys often run to support their juvenile and infant offspring when these individuals scream during rough play.<sup>12</sup> An experiment in which peripheral skin temperature was measured in chimpanzees while they were shown emotionally laden videos reported a decrease of skin temperature, indicative of negative sympathetic nervous system arousal, when subjects viewed videos of conspecifics injected with needles or videos of the needles themselves, but not when they viewed videos of a conspecific chasing the veterinarian.<sup>13</sup> Thus, when chimpanzees perceive meaningful emotional stimuli, they are subject to physiological changes similar

to those observed during fear in humans, that is, to the dispositional effects of emotional contagion.<sup>14</sup>

### The role of social attachment

Social attachment serves intrinsically important regulatory functions of security, nurturing, and distress alleviation. The animal data on maternal care and nurturance suggest that primitive empathic ability might be organized by basic biological systems subserving a complex of attachment-related processes. The neural systems supporting attachment include multisensory processing and complex motor responses as well as cognitive processes that link sensory inputs to motor output, including attention, memory, social recognition, and motivation.<sup>15</sup> A functional network involving preoptic areas of the hypothalamus, ventral septum, and diencephalic and midbrain systems<sup>7</sup> may change somewhat in phylogenesis with more contribution of paralimbic areas, as evidence supports that in primates, ACC and nucleus accumbens are increasingly critical for attachment and maternal behavior.<sup>16</sup> In mammals, neuropeptides regulating attachment, particularly oxytocin, opioids, and prolactin, are relevant for regulating empathic responsiveness. Oxytocin facilitates maternal behavior and is capable of increasing positive social behaviors, and both oxytocin and social interactions reduce activity in the HPA axis.<sup>17</sup> Secretion of hormones of the HPA axis (cortisol, corticosterone, or adrenocorticotrophic hormones) follow separation from the attachment figure, and HPA activity tends to decline upon reunion. Oxytocin targets are widespread and include the hypothalamus, amygdala hippocampus, brainstem, heart, uterus, and regions of the spinal cord that regulate the autonomic nervous system, especially the parasympathetic branch.<sup>18</sup>

While the HPA modulatory effects of oxytocin are species specific, in recent years, a number of studies have clearly reported its implication in human social cognition and empathy. In particular, its application via nasal spray reduces responses to social stress.<sup>19</sup> Oxytocin can increase mutual trust, and this effect is not due to a general increase in the readiness to bear risk. On the contrary, oxytocin specifically affects an individual's willingness to accept social risks arising through interpersonal interaction.<sup>20</sup> Intranasal administration of oxytocin, compared to placebo, reduces amygdala activation and modulates its coupling with brainstem regions that are involved in

automatic fear reactivity.<sup>21</sup> Another study showed that a single dose of intranasally administered oxytocin is sufficient to cause a substantial increase in the ability in affective mentalizing ability on a test relying on the detection of subtle affective facial expressions.<sup>22</sup> There is evidence that a naturally occurring genetic variation of the oxytocin receptor relates to both empathy and stress profiles. This was discovered in a study that tested how a polymorphism (rs53576) of the oxytocin receptor relates to empathy and stress reactivity.<sup>23</sup> Compared with individuals homozygous for the G allele of rs53576 (GG), individuals with one or two copies of the A allele (AG/AA) exhibited lower behavioral and dispositional empathy.

All of these results concur with animal research suggesting a critical role of oxytocin in prosocial approach behavior and reactivity to social stress. It has also been proposed that the interaction between oxytocin and dopamine enhances the reward of social encounters, promoting the motivation to engage in social interactions, thereby increasing the probability of approach and decreasing the probability of withdrawal.<sup>15</sup>

Research on human parenting behavior suggests that networks of highly conserved hypothalamic–midbrain–limbic–paralimbic–cortical circuits act in concert to support aspects of parent response to infants, including the emotion, attention, motivation, empathy, and other thinking processes that are required to navigate the complexities of parenting.<sup>24</sup> Specifically, infant stimuli activate basal forebrain regions, which regulate brain circuits that handle specific nurturing and caregiving responses and activate the brain's more general circuitry for handling emotions, motivation, attention, and empathy—all of which are crucial for effective parenting.

In humans, there is solid behavioral evidence demonstrating that attachment security provides a foundation for empathic concern and caregiving. A series of studies that examined the causal effect of chronic and contextual activation of attachment security on reactions to others' needs<sup>25</sup> indicated that attachment security priming facilitates empathy responses toward others' plights, even when the individuals are not aware of the manipulation (subliminal priming). Furthermore, the sense of security led participants to adopt a more empathic attitude not only to close relationship partners, but also to non-intimate others. Conversely, personal distress, which

may be induced from affective arousal and emotion contagion, can interfere with empathic concern in depleting attentional and cognitive resources to attend to others' needs and to provide adequate care to alleviate their suffering.<sup>26,27</sup> This shows that affective arousal does not necessarily lead to concern for the well-being of others. Affect regulation linked to attachment security plays a crucial role in the motivation to help by reducing personal distress and avoidance behaviors.

### Neural circuits implicated in the perception of others' distress

The long history of mammalian evolution has shaped maternal brains to be sensitive to signs of suffering in one's own offspring.<sup>28</sup> In many primates, as well as many mammals, this sensitivity has extended beyond the mother–child relationship, so that all normally developed individuals dislike seeing others suffering. Pain serves evolved protective and survival functions not only by warning the suffering individual, but also by impelling expressive behaviors that attract the attention of others.<sup>29</sup>

A handful number of studies have recently demonstrated that rodents show social modulation of emotional responses and learning. In one such study, pain sensitivity was found to be modulated in mice by the presence of other mice showing pain response, and this mechanism operates only between cage mates and not strangers.<sup>30</sup> To investigate whether such pain-related behavior can serve the function of soliciting social approach, the same authors used a social approach paradigm to test mice in various dyadic or triadic conditions, including “jailed” mice—some in pain via intraperitoneal injection of acetic acid—and test mice free to approach or avoid the jailed mice.<sup>31</sup> Results showed a sex-specific effect whereby female, but not male, test mice approached a familiar same-sex conspecific in pain more frequently than an unaffected familiar or unfamiliar, but affected, conspecific. Furthermore, the frequency of contact by the test mouse was negatively correlated with the pain behavior of the jailed mouse, suggesting that proximity of a familiar unaffected conspecific may have analgesic properties. Using pharmacological and genetic manipulations, a recent experiment found that the lateral nucleus of the amygdala is essential for both the acquisition and expression of observational fear.<sup>32</sup> While inactivation of the lateral pain system had no influence on

observational learning, inactivating any component of the medial pain system (ACC or mediodorsal nuclei) during learning blocked the acquisition of fear, whereas inactivating them only before memory retrieval did not block fear expression. These results suggest that the medial system is essential for transmitting the aversive nature of the situation to the amygdala during observational learning.

In keeping with the thalamocingulate hypothesis of maternal behavior in humans, it has been found that mothers listening to infant cries show increased activity in the medial thalamus, insula, subgenual ACC, and OFC, as well as in structures important in rodent maternal behavior, such as the midbrain, hypothalamus, dorsal and ventral striatum, and vicinity of the lateral septal region.<sup>33</sup>

A growing number of fMRI studies have demonstrated that the same neural circuit—the so-called pain matrix—that is involved in the first-hand experience of pain is also emulated by the anticipation,<sup>34,35</sup> perception,<sup>36–43</sup> or imagination<sup>44,45</sup> of other individuals in pain. This neural network includes the supplementary motor area (SMA), dorsal ACC, anterior medial ACC (aMCC), AIC, amygdala, and periaqueductal gray matter (PAG) (Fig. 2) (see Refs. 46 and 47 for meta-analyses).

It is worth noting that vicariously instigated activations in the pain matrix are not necessarily specific to the emotional experience of pain, but are related to other processes such as negative stimulus evaluation, attention to noxious stimuli, somatic monitoring, and the selection of appropriate skeletomuscular defensive movements.<sup>48,49</sup> Several electroencephalography and fMRI studies have documented extremely similar patterns of responses to nociceptive and non-nociceptive stimuli, suggesting that multimodal neural activity (i.e., the activity of neurons that respond to a range of stimuli, regardless of their sensory modality) could explain a large part of the pain matrix.<sup>50</sup>

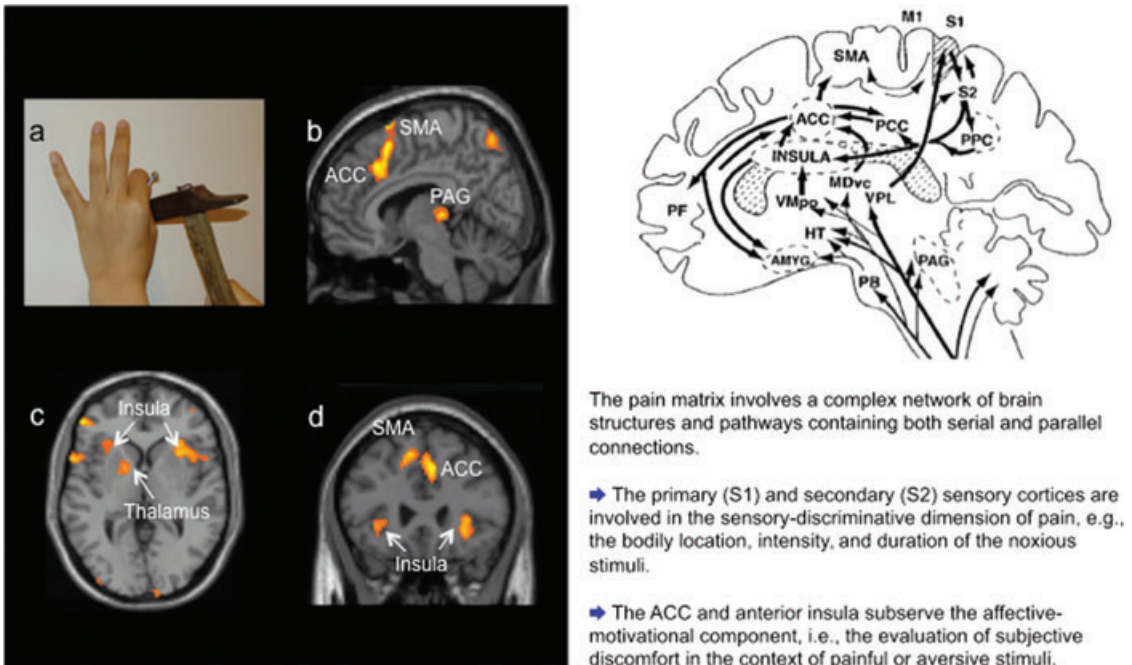
Of particular importance, activation of the AIC is the most robust evidence across all studies of pain empathy: this response can even be elicited automatically, independent from explicit task requirements.<sup>51</sup> It has been proposed that the anterior insula, through its intimate connections with amygdala, hypothalamus, ACC, and OFC, serves to compute a higher-order metarepresentation of the primary interoceptive activity, which is related to the feeling of pain and its emotional awareness.<sup>52</sup>

These representations play an important role in the learning and adaptation of prosocial behavior, and they may guide decision making and homeostatic regulation.<sup>53</sup> The sharing of vicarious negative arousal, which crucially involves the anterior insula and ACC, provides a strong signal that can promote empathic concern. To be motivated to help another, one needs to be affectively, empathically aroused, and to anticipate the cessation of mutually experienced personal distress.

### Empathy is a flexible adaptive phenomenon

Empathy is not automatic or reflexive, and many factors affect its induction and expression. As mentioned above, rodents do not react indiscriminately to other conspecifics in distress. Recent studies with human volunteers have documented that the neural network implicated in empathy for pain is modulated by various social and interpersonal factors. For instance, one fMRI study demonstrated that empathic arousal is moderated early in information processing by *a priori* attitudes toward other people.<sup>54</sup> Study participants were significantly more sensitive to the pain of individuals who had contracted AIDS as the result of a blood transfusion as compared to individuals who had contracted AIDS as the results of their illicit drug addition (sharing needles), as evidenced by significantly higher pain and empathy ratings and significantly greater hemodynamic activity in areas associated with pain processing (i.e., AIC, aMCC, PAG). Activity in that network is enhanced when people viewed their loved ones in pain compared to strangers<sup>44</sup> and is reduced if the person in pain has been unfair in a prior interaction<sup>55</sup> or is from a different ethnic group.<sup>56</sup>

Empathic arousal is also modulated by an individual's knowledge and experience with pain. Two neuroimaging studies directly investigated how physicians react to the perception of others' pain. One study compared the neuro-hemodynamic response in a group of physicians and a group of matched control participants while they viewed video clips depicting face, hands, and feet being pricked by a needle (painful situations) or being touched by a Q-tip (non-painful situations).<sup>57</sup> The results demonstrated activation of the pain matrix in the controls when they attended to the painful situations relative to the nonpainful ones. A different pattern of signal change was detected in the physicians



**Figure 2.** Neural networks involved in perceiving others in distress and pain largely overlap with the processing of nociceptive information. Neurophysiological research on pain processing points out a distinction between the sensory-discriminative and the affective-motivational domains. The former domain engages stimulus localization and is assessed with ratings of intensity while the latter one involves the affective component of pain and is measured with ratings of unpleasantness. This duality is also framed in terms of medial and lateral thalamic processing and extent for cortical structures, including somatosensory and anterior cingulate cortices, respectively, based on thalamic afferents. These two dimensions of pain processing are underpinned by discrete yet interacting neural networks. A growing number of neuroimaging studies recently demonstrated that the perception of pain in others recruits brain areas chiefly involved in the affective and motivational processing (ACC, insula), as well as the somatosensory cortex and PAG. The anterior insula lies between the lateral and medial systems and is involved in processing associated with each system, including sensory coding, body state assessment, and autonomic regulations as well as emotional valence coding of sensory events. The cingulate cortex mediates the three aspects of pain processing that may use affect regulation but is explicitly involved in avoidance/nocifensive behaviors.

when they watched painful procedures. Cortical regions underpinning executive functions (dorso-lateral and medial prefrontal cortices) and executive attention (precentral gyrus, superior parietal sulcus and temporo-parietal junction) were found to be activated, and unlike in the control group, no signal increase was detected in the pain matrix. A second study recorded event-related potentials (ERP) from physicians and matched controls as they were presented with the same visual stimuli.<sup>58</sup> The results showed early N110 differentiation between pain and no pain, reflecting negative arousal, over the frontal cortex, as well as late P300 over the centro-parietal regions in control participants. In contrast, no such early ERP response was detected in the physicians. This indicates that affect regulation and context in physicians has very early effects,

inhibiting or appraising the bottom-up processing of negative arousal arising from the perception of painful stimuli, and thus, may have beneficial consequences in freeing up cognitive resources necessary for being of assistance and express empathic concern. There may be a cost though for practitioners dampening their sensitivity to the pain and affective reactions of their patients. A modicum of negative arousal seems necessary to help physicians attune to and empathically understand patient's emotions. This important issue requires further investigation as the medical profession is struggling to achieve an appropriate balance between clinical distance and empathic concern.<sup>59</sup>

Thus, incoming sensory information is constrained by appraisal and reappraisal, processing, which may be unconscious or conscious, and shapes

the emergence of the experience of empathy and behavioral outcomes. The dampening of “state” reactivity influences the availability of higher brain structures involved in regulating behaviors.

### What is specific to human empathy?

Like in other mammalian species, emotions and feelings may be shared among individuals, elicit alarm or fear, and, at times, facilitate empathic concern. Humans, however, can imagine what others feel, and more importantly, can intentionally “feel for” and act on behalf of other people whose experiences may differ greatly from their own.<sup>60</sup> Empathic concern is often associated with prosocial behaviors and has been considered as a chief enabling process for altruism.<sup>1</sup> When people send money to distant earthquake victims in Haiti, or petition to support a bill that would contribute to curb the violence in Darfur, empathy reaches beyond its context of evolutionary origins, extending beyond inclusive fitness benefits among kin. Humans can feel empathic concern for a wide range of others in need, even dissimilar others.<sup>43</sup> Empathic helping behavior may have also evolved because of its contribution to genetic fitness,<sup>61</sup> and an impulse to care for offspring is almost certainly genetically hardwired in humans as well as in other mammals. Once the empathic capacity evolved, following the principle of motivational autonomy (i.e., motivation for a given behavior becomes disconnected from its ultimate goals), it could be applied outside the parental-care context.<sup>11</sup> Moreover, empathy is assisted by other abstract and domain-general high-level cognitive abilities such as executive functions, language, and perspective taking, which expand the range of behaviors that can be driven by empathy.

Perspective taking plays a critical role in empathic concern as well as emotion regulation. For example, Batson and his colleagues found that when participants are told of another individual’s plight and asked to imagine how that person feels, empathic concern is elicited.<sup>62</sup> However, when the same individuals are asked to imagine instead how they would feel in the place of the other person, feelings of anxiety and personal distress are evoked. To test this hypothesis, an fMRI study presented participants with video clips of individuals expressing pain on their face, due to a medical treatment.<sup>63</sup> Participants were instructed to either imagine how they would themselves feel if they were in the patient’s

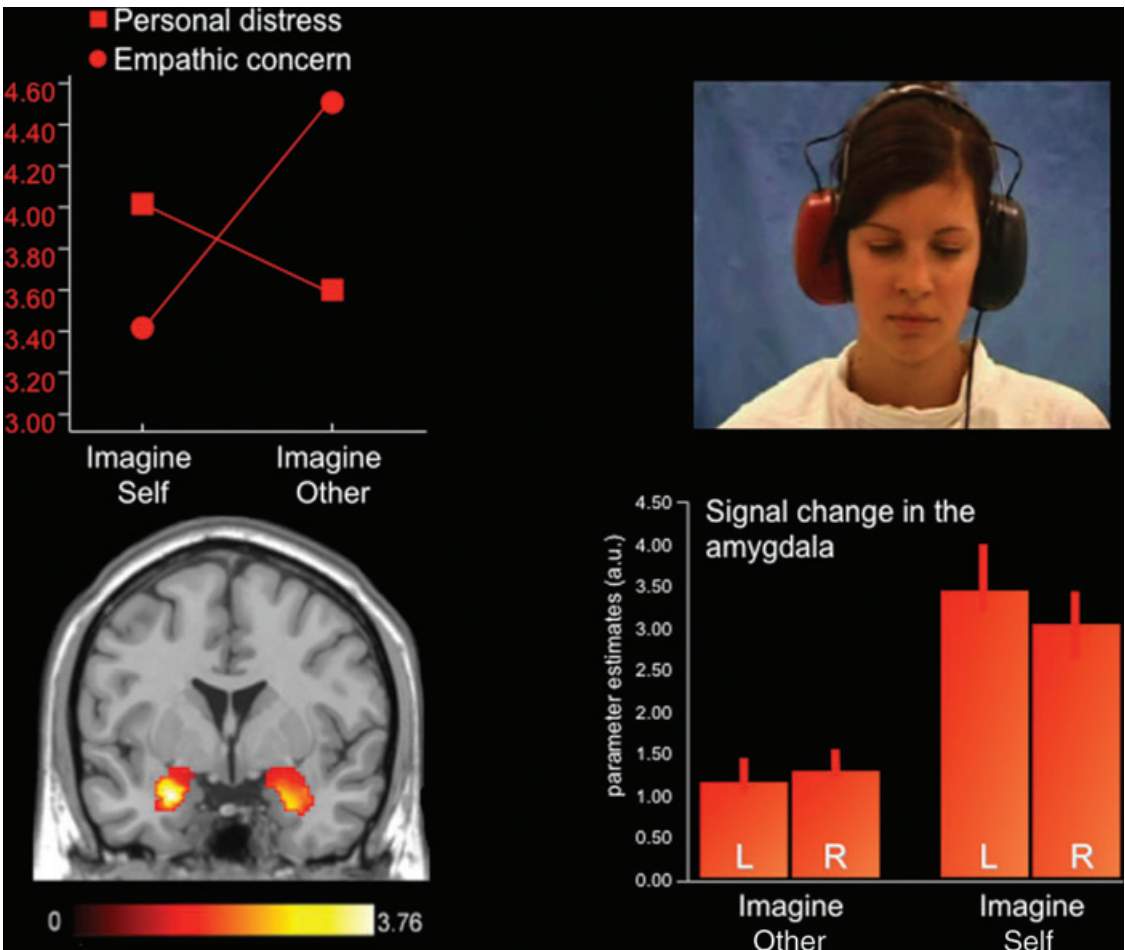
situation (imagine self), or imagine what the patient was feeling (imagine other). The former subjective perspective was associated with a strong hemodynamic increase in the amygdala, as well as subjective reports of anxiety and personal distress. When the participants were imagining what the patients were feeling, decreased activity was detected in the amygdala, with reduced feelings of anxiety combined with increased reports of empathic concern (Fig. 3).

Does this mean that these most advanced forms of empathy are operating independently from more basic neurobiological mechanisms? Probably not. For example, thinking about movement hurts in people with chronic arm pain.<sup>64</sup> When patients imagined moving their arm to match the postures shown in pictures, pain and swelling ( $8 \pm 5\%$ ) was greater posttask than pretask. However, the change in pain and swelling was related to catastrophizing and fear of movement, and also to autonomic arousal early in the task. Real-time inflammatory responses can be mediated by the autonomic nervous system, which also interacts closely with limbic systems important in memory.

### An evolutionary continuity

There is an evolutionary continuity in the neurobiological systems that provide the basis for empathy and caring. The relations between emotion, empathic concern, and prosocial behavior operate on a series of nested evolutionary processes, which are intertwined with social, motivational contingencies, and also subject to contextual control. For instance, within a social group and contingent on cognitive interpretation, perceiving in pain or distress triggers a neural response associated with aversion. This physiological arousal, in turn, may initiate helping or soothing behaviors motivated by a plurality of motives, including reducing one’s own discomfort, feeling good about oneself, or feelings of sympathy for, or compassion for the other with the ultimate goal to lessen his or her distress. These behaviors are reinforced both by endogenous reward (dopamine system) as well as positive social feedback from others. Behavioral and functional neuroimaging studies have demonstrated that being nice and caring for others makes us feel good by the release of dopamine through the projection of neural pathways from the brainstem to the nucleus accumbens. The fronto-mesolimbic reward network is engaged to the same extent when individuals





**Figure 3.** Impact of language and imagination in eliciting empathic concern or personal distress. Hemodynamic signal change in the amygdala (left and right) resulting from different verbal instructions given to study participants while they were watching video clips of people in pain due to a medical acoustic treatment (the patients in the videos were exposed to painful sound). When the subjects imagined how they would feel in the patient’s situation (an imagine self-perspective), a strong hemodynamic increase was detected in the amygdala, as well as subjective reports of anxiety and personal distress. When the participants imagined how the patient was feeling (an imagine other perspective), decreased activity was observed in the amygdala in conjunction with reduced feelings of anxiety combined with increase reports of sympathy and concerns for the patient. In addition to the signal change in the amygdala, imagining oneself in pain compared with imagining the other was associated with the increase in the insula, SMA, and parietal cortex. Adapted from Ref. 63.

receive monetary rewards and when they freely choose to donate money to charitable organizations.<sup>65</sup> Furthermore, medial orbitofrontal-subgenual and lateral orbitofrontal areas, which play key roles in more primitive mechanisms of social attachment and aversion, mediate decisions to donate or to oppose societal causes. Another fMRI study reported that the mere presence of observers increased donation rates and significantly affected activity in the striatal regions.<sup>66</sup> The cerebral functions that de-

veloped originally in service of parental nurturance in the mammalian species continued to evolve, accompanied by an increase in the plasticity and flexibility provided by the prefrontal cortex, which led in turn in a heightened capacity for learning and came to operate at the level of the social group and cultural level.

Overall, this evolutionary conceptual view of empathy is compatible with the hypothesis that advanced levels of social cognition have arisen



as an emergent property of powerful executive functioning assisted by the representational properties of language.<sup>67</sup> These higher levels operate on previous levels of organization and should not be seen as independent of, or conflicting with, one another. Evolution has constructed layers of increasing complexity, from nonrepresentational (e.g., affective arousal, emotion contagion) to representational and metarepresentational mechanisms, operating in both hierarchical and parallel fashion. The evolutionary development of newer neural system confers greater behavioral flexibility and variability, but does not replace older mechanisms. Furthermore, information is processed and responses are organized across multiple levels, from lower-level systems that are rapid, efficient, but rigid, to higher-level systems that are integrative and flexible.<sup>68</sup> Cognitive, sensorimotor, and somatovisceral mechanisms are intimately connected, as stressed by embodied cognition and simulation models,<sup>69,70</sup> and older systems are co-opted by newer systems. Similar systems that regulate parental behavior and affective processing interact with newer cortical systems to produce the flexible and generalized forms of nurturant care found among humans. On the one hand, this explains why humans care not only for their offspring and in-group members but also for strangers, and can also be motivated to uphold moral principles such as justice and fairness. On the other hand, one finds implications of the interaction between ancient evolutionary mechanisms and newer ones, subserving unique aspects of the human mind, in that ideologies, religious ideas can filter out, dampen, or inhibit our empathy for fellow human beings.

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### Conflicts of interest

The author declares no conflicts of interest.

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