



The empathic brain: how, when and why?

Frédérique De Vignemont, Tania Singer

► To cite this version:

Frédérique De Vignemont, Tania Singer. The empathic brain: how, when and why?. Trends in Cognitive Sciences, Elsevier, 2006, 10 (10), pp.435-441. <ijn_00169584>

HAL Id: ijn_00169584

http://jeannicod.ccsd.cnrs.fr/ijn_00169584

Submitted on 4 Sep 2007

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

The empathic brain: how, when and why?

Frederique de Vignemont¹ and Tania Singer²

¹ Institut des Sciences Cognitives, 67 bd Pinel 69675 Bron cedex, France

² Center for Social Neuroscience and Neuroeconomics, Institute for Empirical Research in Economics, University of Zürich, Blümliisalpstrasse 10, CH – 8006 Zürich, Switzerland

Recent imaging results suggest that individuals automatically share the emotions of others when exposed to their emotions. We question the assumption of the automaticity and propose a contextual approach, suggesting several modulatory factors that might influence empathic brain responses. Contextual appraisal could occur early in emotional cue evaluation, which then might or might not lead to an empathic brain response, or not until after an empathic brain response is automatically elicited. We propose two major roles for empathy; its epistemological role is to provide information about the future actions of other people, and important environmental properties. Its social role is to serve as the origin of the motivation for cooperative and prosocial behavior, as well as help for effective social communication.

Introduction

Ten years after the discovery of mirror neurons in monkeys [1], we now also have evidence for shared affective neuronal networks underlying our ability to empathize. Brain imaging studies have shown overlapping brain activation patterns when subjects feel their own emotions and observe the same emotions in others [2–8]. It has been suggested that: (i) shared affective neuronal networks explain how we feel the emotions of others as if they were our own and (ii) these networks are activated automatically whenever we observe others displaying emotion. But is empathy really automatically triggered every time we observe someone else displaying emotion? Here, with the combined perspectives of neuroscience, psychology and philosophy, we question the assumption of automatic empathy and propose several factors that might modulate when and to what extent we feel empathy. In addition, we provide preliminary answers to the question concerning why empathy might have evolved.

What is empathy and how do we empathize: the shared network hypothesis

Before suggesting some answers to the how, the when and the why of empathy, we attempt to shed light on what empathy means. There are probably nearly as many definitions of empathy as people working on the topic. There are two main trends: some argue for a broad definition of

empathy as an understanding of another person's feelings, affect sharing [9] or as 'an affective response more appropriate to another's situation than one's own' [10]. So defined, empathy subsumes phenomena such as emotional contagion, sympathy, personal distress or even cognitive perspective-taking. However, this definition does not enable precise claims to be made about the nature of empathy or its automaticity because one can always reply that it depends on the level of empathy [11]. Others, ourselves included, prefer to narrow down the concept of empathy [12,13]. There is empathy if: (i) one is in an affective state; (ii) this state is isomorphic to another person's affective state; (iii) this state is elicited by the observation or imagination of another person's affective state; (iv) one knows that the other person is the source of one's own affective state.

This narrower definition of empathy still leaves some questions open (Box 1). However, it enables us to distinguish empathy from other related phenomena. Cognitive perspective-taking, for example, does not meet the first condition. One represents the mental states of others, including affective states, without being emotionally involved (e.g. based on my knowledge of you, I infer from your behavior that you are anxious but I do not feel anxious). Similar to empathy, sympathy refers to an affective state related to the other and is therefore often taken as being synonymous [13]. However, it does not meet the condition of isomorphism (e.g. I feel sorry for you because you feel jealous, depressed or angry but I am not jealous or depressed myself). Finally, emotional contagion involves affect sharing but does not meet the condition of self–other distinction (e.g. the baby starts crying because other babies cry but the baby is not necessarily aware that the other is the source of their affective state).

The narrow definition of empathy proposed above was partially motivated by the investigation of the neuronal basis of empathy. Recent functional magnetic resonance imaging (fMRI) studies have shown that observing another person's emotional state activates parts of the neuronal network involved in processing that same state in oneself, whether it is disgust [2], touch [3] or pain [4–8] (Figure 1).

Some authors have suggested that shared circuits such as these are formed by associative learning or Hebbian learning mechanisms in the domains of actions [14,15], emotions and sensations [15]. In the view of these authors, shared networks might result from associations between simultaneously firing, coactivated neurons. Hence,

Corresponding author: Singer, T. (singer@iew.unizh.ch).
Available online 1 September 2006.

Box 1. Open questions about empathy: consciousness and isomorphism

Controversy exists as to whether empathic responses are necessarily conscious. Some philosophers argue that empathy is a conscious experience of what it is like to feel what the other feels through 'online simulation' [43,44]. By contrast, neuroscientists promote the view that affective states are automatically and unconsciously shared with others. Although it is possible to study empathy independently of this problem, this phenomenological dimension still remains to be acknowledged.

Another open question concerns the degree to which the empathic response is isomorphic to the original affective state. Is it a coarse-grained congruency (e.g. only the same valence) or a more fine-grained equivalence (e.g. same valence, intensity and components)? Neuroscience has started to tackle this question but cannot yet provide an unambiguous answer. Most of the recent fMRI studies on pain, for example, have suggested that empathic responses are associated with activity in the affective component of the pain network (ACC and AI) rather than with its sensorimotor properties (primary and secondary somatosensory cortices). However, using transcranial magnetic stimulation, Aglioti's group revealed reduced motor excitability specific to the muscle that the subjects observed being penetrated deeply by needles in another person [21]. Likewise, a recent study of 'empathy' for touch revealed activation of primary sensorimotor cortex that was somatotopically mapped [45], contrasting with another study showing only secondary somatosensory cortex activity [3]. A challenge for future research will be to isolate the factors determining the degree of isomorphism in empathy.

whenever a percept (e.g. the sight of an angry face) or symbolic cue (e.g. the word 'pain') is accompanied by a certain emotional, visceral or somatosensory activation, a connection between the cue and the neural representation of the internal sensation is formed. Later, the mere presentation of these cues can trigger the emotional, visceral or sensorimotor representation associated with it. According to this view, empathic responses are automatically elicited by the mere perception of these cues. But is empathy really always automatic?

When do we empathize: automatism and modulatory factors

As Figure 1 illustrates, common neural networks involved in empathy are activated by the perception not only of loved ones in pain [4], but also of unknown people in pain [8], or even of a needle penetrating the back of someone's hand [6]. Furthermore, subjects have not always been told the goal of the study [2–4,6,7]. These results suggest that we always automatically empathize with others when exposed to their emotions, regardless of who they are. Is this true? Or are we more selective?

At the phenomenological level, we are obviously not constantly empathizing with the people around us [16]. In real life, we constantly witness people displaying contradictory emotions. If we were to consciously feel what they feel all the time, we would be in permanent emotional

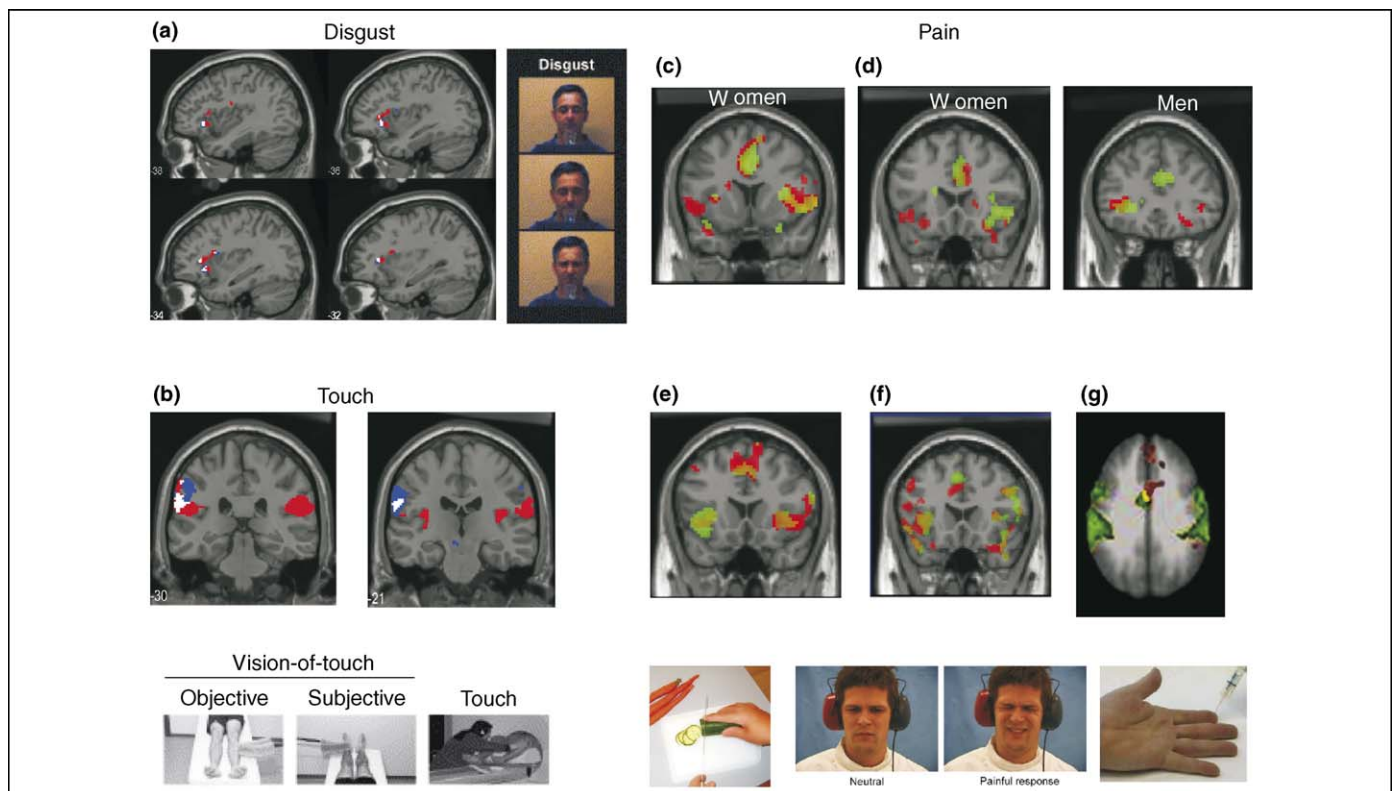


Figure 1. Shared brain networks, as revealed in fMRI studies on empathy for disgust, touch and pain. (a) A common brain activation in the AI elicited by the smell of disgusting odors (red) and the sight of someone else smelling disgusting odors [2]. (b) Common activation in SII associated with being touched on a leg (red) or watching videos showing a leg being touched (blue) [3]. (c–g) Overlapping brain activity in the AI and ACC when receiving painful stimulation oneself (green) or when empathizing with another person feeling pain (red), whereby (c) shows the activation of women perceiving cues indicative of their male partners feeling pain [4], (d) depicts the involvement of the same network when women (right) or men (left) observe an unknown but previously fair player receiving painful stimulation [22] and (e–g) illustrate brain responses of subjects viewing still images of potentially painful situations [50], facial expressions of pain [8] and needles pricking a human hand [6]. For all further details regarding methods and analysis of these studies, see papers cited.

Box 2. Motor theory of empathy

The notion of empathy has been linked to action ever since it was introduced. Theodor Lipps suggested that by internally imitating a facial expression, we have direct access to the emotion that triggered that facial expression. The discovery of mirror matching systems in the motor domain is considered as the first neural evidence of Lipps' theory: the perception of someone else moving suffices to elicit a mental simulation of the observed movement and, if not inhibited, the subsequent physical execution of that movement. Imitation is thus a prepotent automatic response tendency [14], even if usually inhibited.

One might then suggest that empathy is not so far from imitation. They both depend on shared representations between self and other. They are both automatic. They both remain offline if inhibited. Consequently, several authors propose a 'motor theory of empathy' [46–49] according to which one recognizes others' emotions by means of action representation and imitation: emotions can be expressed by gestures and/or facial expressions (i.e. actions), and internally mimicking these actions enables one to recognize the underlying affective states.

We propose that empathy does not rely exclusively on bodily movements. Consequently, neuronal networks underlying empathy do not necessarily activate the usual motor circuitries observed in action observation and imitation. As Figure 1 illustrates, empathic responses activate somatosensory cortices as well as limbic and paralimbic structures such as the ACC and AI instead of action systems associated with mirror neurons. These findings suggest that one can rely on the shared emotional network alone, independently of any activation of the motor network. Although mirror systems are domain specific [38], action can still be viewed as a model of understanding [9].

turmoil, leaving no room for our own emotions. However, from a neuroscientific perspective, it could be argued that we unconsciously share the affects of others even though we are not aware of doing so. The question of when we empathize would thus be irrelevant because empathic brain responses would be automatic and systematic [9]. In this sense, empathy would not differ from emotional contagion or imitation (Box 2).

We now provide neuroscientific evidence suggesting that empathy is not merely the consequence of the passive observation of emotional cues but that it is subject to contextual appraisal and modulation. Such a view is in line with several years of behavioral research in the fields of developmental and social psychology investigating the role of modulatory factors, such as similarity and familiarity, in empathy, mostly measured indirectly through indices of prosocial behavior or self- and parental reports [9,17–20].

Modulation of the empathic brain

Recently, neuroscientists have started investigating whether activity in shared emotional networks can be

modulated. Evidence for a modulatory role of saliency and intensity of the pain stimulus was observed by Aglioti's group, who only saw an empathy-related reduction in motor excitability in the observer's hand when a needle deeply penetrated the model's muscle but not when the needle merely pricked the hand [21].

Singer *et al.* [22] found modulation as a function of the affective link between the empathizer and the person in pain. Male and female volunteers first played repeated sequential Prisoner's Dilemma games with two confederates. One confederate played fairly and the other unfairly. Empathy-related activation in the anterior cingulate cortex (ACC) and anterior insula (AI) was observed for both genders when the fair, likeable player was in pain. However, men, but not women, showed an absence of such empathic activity when perceiving an unfair player in pain. Instead, the men showed, on average, an increase in activity in areas associated with reward (nucleus accumbens), which was positively correlated with the expressed desire for revenge assessed after the study by questionnaires. Finally, Lamm *et al.* [23] showed that subjects had a smaller empathic response in pain-related areas when they knew that the pain inflicted to the other was justified to cure the other, than when not [23]. In sum, these findings suggest that empathic brain responses are prone to modulation.

The contextual approach

Based on these findings, we propose a contextual approach to empathy. We propose that: (i) empathy is modulated by appraisal processes and (ii) this modulation is present even at the subpersonal level of a neural empathic response, and can be fast and implicit.

First, we distinguish between two types of modulation of empathy. On the one hand, one can modulate one's empathy voluntarily, using the control one has over one's emotional responses [24]. For example, medical practitioners or Buddhist monks can acquire high degrees of emotional control with experience and practice. On the other hand, empathy can be modulated by implicit appraisal processes, which might strongly influence the magnitude of empathic responses. We now focus on the latter aspect and distinguish between four main categories of modulatory factors (Table 1).

Intrinsic features of the shared emotion

The intensity, saliency and valence (positive versus negative) of the emotion displayed by the target might have a great influence on the intensity of the empathizer's empathic response. Moreover, it might be easier to

Table 1. Modulatory factors of empathy

Features of emotions	Relationship between empathizer and target	Situative context	Empathizer
Valence	Affective link and nurturance	Appraisal of the situation	Mood arousal
Intensity	Self-implication (e.g. jealousy, anger)	Display of multiple emotions	Personality, gender and age
Saliency	Familiarity and similarity		Emotional repertoire
Primary versus secondary emotions	Communicative intentions		Emotional regulation capacities

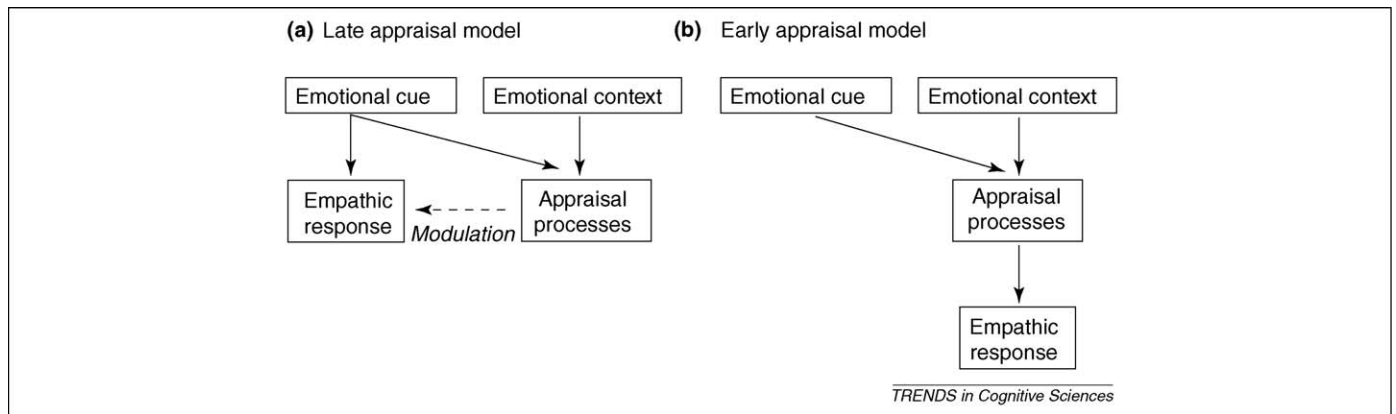


Figure 2. Schematic representation of the early and late appraisal model of empathy.

empathize with primary emotions such as fear, happiness or sadness than with secondary emotions such as jealousy.

Relationship between the empathizer and the target

In the study by Singer *et al.* [22], the empathic responses were modulated by the affective link between the empathizer and the person in pain. Other factors, such as similarity [18], familiarity [19] between the two protagonists, how much protection or care (e.g. nurturance [20]) the target needs and whether the emotion is directed towards the empathizer or not (the person in pain being angry or jealous about the empathizer) might also be crucial.

Characteristics of the empathizer

The gender [25,26], personality, age [27] and past experiences of the empathizer [28] might be relevant. An empathizer who does not suffer from vertigo can hardly empathize with a target who is frightened by the void below him because he does not have the specific feeling of vertigo in his repertoire. In such a case, the empathizer might engage in cognitive perspective-taking rather than empathizing.

Situative context

Could I share your joy if I knew that it was not justified? Could I empathize with you if you suddenly started crying for no apparent reason or would I be more surprised? Empathizing can also become difficult if the empathizer is simultaneously confronted with two or more targets if the targets are expressing different emotions.

Some of the modulatory factors can be partly explained by the role they have in increasing or decreasing attention to the emotion-eliciting stimulus (e.g. cue saliency and intensity; empathizer's mood and level of arousal; empathizer and target's familiarity with and similarity to each other; target's intention to communicate that he wants the empathizer to share his emotions). However, the modulation of empathy cannot solely be explained by attention. In the study by Singer *et al.* [22], for example, men paid as much attention to fair as to unfair players, as shown by a similar degree of brain activity at the sight of nonpainful stimulation of both players. Future research will have to determine the relative importance of these factors and investigate their complex interplay in modulating empathic brain responses.

When does modulation occur?

The next question that arises is, at which stage of empathic processing does this modulation occur? Do appraisal processes take place before the onset of, or during an empathic response? Figure 2 illustrates the two possible routes.

According to the late appraisal model, the empathic response is directly and automatically activated by the perception of an emotional cue. The default rule is that there is always an empathic response. However, this model does not prevent the prior empathic response from being modulated or inhibited at a later stage. Information about the general and personal context is processed in parallel. The outcome of the contextual appraisal process leads to the modulation of the empathic response. This modulation can either be achieved by top-down inhibitory or excitatory processes or by horizontal competition between different motivational processes. For example, in the study by Singer *et al.* [22], different motivational systems might have competed and the men's desire for revenge might have won over the inclination to empathize with someone feeling pain. Thus, in this model, there are two independent systems working in parallel, empathic resonance and appraisal processes.

According to the early appraisal model, the empathic response is not directly and automatically activated by the perception of an emotional cue. Rather, the emotional cue is evaluated in the context of external and internal information. Whether an empathic response is elicited depends on the outcome of the contextual appraisal process. Thus, the default rule is that an empathic response is not automatically activated but an empathic response might be elicited as the outcome of the appraisal process (Jacob and Jeannerod [29] have a similar view of mirror neurons).

Current neuroscientific studies on empathy cannot yet distinguish between these two proposed routes. The results of Singer *et al.* [4] provide an example of a case in which contextual processing preceded the activation of shared networks. Subjects had to decode a symbolic colored cue indicating whether a painful or nonpainful stimulation would be delivered to the other person. Only then could they engage in empathy. In the future, additional studies should be designed that distinguish between the two routes proposed above (Box 3). One possibility would be to use alternative techniques, such as electro- or

Box 3. Questions for future research

- What are the temporal dynamics of empathic brain responses and their modulation?
- How can neuroscience explain the influence of modulatory factors on shared emotional networks?
- How do empathy, sympathy, prosocial behavior and cognitive perspective-taking relate to each other?
- Does brain architecture constrain which shared emotional networks can be formed?
- How does the brain differentiate between self and other?
- How does the awareness of empathic responses arise? Is it associated with a dimensional shift in the brain activation threshold in the shared brain network or a qualitatively different pattern of neural activation?
- Is there evidence for a failure in, or disruption of, shared emotion networks in people with social deficits, such as people with autistic spectrum disorder and psychopathy?
- Is there evidence for neuronal plasticity in the domain of social emotions like empathy?

magnetoencephalography, which provide a better temporal resolution than fMRI. Moreover, paradigms such as that used by Singer *et al.* [22] could be improved by analyzing the effective connectivity (e.g. by dynamic causal modeling [30]); this would enable the determination of whether the decrease in empathy-related activation in the ACC and AI in men observing unfair as compared with fair players in pain was causally preceded by an increase in activation in the dorsolateral prefrontal cortex, an area that has been associated with emotional control and inhibition [31,32].

Why do we empathize: epistemological and social roles

Having discussed when we empathize, we now turn to the question of why we empathize. What is empathy for? Here, it is important to distinguish between two questions: (i) why has evolution selected empathy? and (ii) what is the role of empathy now that it has emerged? The former question refers to the adaptive function of empathy, and the answer lies in studies of empathy in other species [9]. The latter question refers to its functional role in everyday life, and the answer lies in studies of disturbances in empathy (e.g. in psychopaths [33]), and in social and developmental psychological studies [17].

With regard to the adaptive function of empathy, some have suggested that empathy was selected by evolution for mother-child bonding [34] or reciprocal altruism [35]. However, neither of these explanations really target empathy specifically because bonding can depend on emotional contagion and altruism on cognitive perspective-taking or sympathy. Moreover, one might argue that empathy does not have a specific adaptive function. Shared emotional representations could have evolved as a byproduct of more general associative learning mechanisms [14,15]. One might even go a step further and propose that shared emotional representations might even be maladaptive and costly. What is the benefit of a mechanism that makes you feel sad whenever someone else is sad? However, given the efficiency of Hebbian learning mechanisms for many other survival functions, it can be argued that the cost associated with empathic responses might simply have been 'tolerated' by evolution.

We will refrain here from any speculation concerning evolution and now focus on the second question by pointing out two major roles of empathy in everyday life, suggesting that empathy is not maladaptive and costly.

Epistemological role

On the basis of the emotions we share with others, empathy enables us to understand what they feel. However, so does cognitive perspective-taking. Also, if we endorse the early appraisal model (Figure 2), empathy might not even be a faster route. So, why is empathy better? We believe that empathy has two main advantages.

First, as compared with cognitive perspective-taking, it might not be the more direct route to understanding other people's emotions but it is a faster route for prediction of their subsequent behavior. We propose that empathy provides a more precise and direct estimate of other people's future actions because shared emotional networks also directly elicit the activation of associated relevant motivational and action systems. By sharing the emotional state of others, we also share their emotional and motivational significance [36]. However, it should be noted that prediction accuracy depends on the similarity between the empathizer's and the target's experiential repertoires [37].

Second, empathy provides knowledge about important environmental properties. For instance, by seeing someone being burnt by a machine, we attach a negative 'avoidance' value to the machine, without first having to experience the pain ourselves [38]. In this sense, empathy is an efficient computation tool for acquiring knowledge about the values of the world around us [9].

Social role

The social role of empathy has been emphasized more in the literature, empathy having been related to moral sense, altruism, justice, prosocial behavior and cooperation [10,27,39,40]. Some behavioral evidence indeed suggests that people help others more when they report having empathized with them, whether they help to alleviate their own personal distress or because they care for the other person [27]. However, it remains to be shown whether individual differences in empathic brain responses also predict subsequent prosocial behavior.

A further question presents itself: is empathy a necessary and sufficient condition for these prosocial behaviors to arise?

Individuals with empathy deficits are more likely to display aggressive, antisocial behavior towards others [10]. Some have even argued that a lack of empathy during development results in a lack of morality [33]. Does this mean that empathy is necessary for prosocial behavior and morality? Empathy has a strong motivational role but it is likely that it is not the only possible motivation for cooperation and prosocial behavior [41]. Imagine, for example, a political prisoner under a dictatorship. Someone might help him to escape, not because he necessarily empathizes with him but because he opposes the government and has strong feelings of hate and beliefs about justice that motivate him to help.

If empathy is not a necessary condition, is it a sufficient condition for inducing prosocial behavior? In line with

others [10,27,40], we suggest that empathy *per se* does not suffice to induce prosocial behavior but that empathy has to be turned into sympathy to motivate helping. By contrast, empathic responses might also result in personal distress and thereby motivate self-related behavior, such as avoidance and withdrawal, instead of other-related prosocial behavior [40]. Clearly, neuroscientific research is still in its infancy. As for questions concerning the interplay between empathy, sympathy and prosocial behavior, we need a better understanding of the neural signature underlying specific emotions and empathy before we can distinguish between empathic and sympathetic affective brain responses.

Finally, we propose that the ability to share other people's emotional experiences and to react to them in a fine-tuned manner might facilitate social communication and create social coherence. For example, in action imitation, the chameleon effect – the tendency to adopt other people's postures, gestures and mannerisms – was found to create affiliation and fondness [42]. Similarly, perceiving another person's empathy for oneself is likely to increase affiliation and strengthen the emotional bond with that person. The development of simultaneous recording techniques between multiple brains might be a promising step for future neuroscientific research in this domain.

Conclusion

Regarding the question of how we share someone else's emotions, this occurs by means of shared affective neural networks, which are activated when we feel our own emotions, as well as when we observe others feeling emotions. Moving on to the question of when we have an empathic response, recent findings suggest that empathic brain responses are modulated by appraisal processes which take into account information about the emotional stimuli, their situative context, characteristics of the empathizer and his/her relationship with the target. With regard to the question of why we feel empathy, we have proposed two major roles of empathy: one epistemological and one social. Empathy might enable us to make faster and more accurate predictions of other people's needs and actions and discover salient aspects of our environment. Furthermore, empathy might serve as the origin of the motivation for altruistic behavior and cooperation. Finally, it might have a crucial role in human communication.

Acknowledgements

We thank Celia Heyes, Chris and Uta Frith, Christian Keysers and the anonymous reviewers for helpful comments on an earlier draft of this paper.

References

- Rizzolatti, G. *et al.* (1996) Premotor cortex and the recognition of motor actions. *Brain Res. Cogn. Brain Res.* 3, 131–141
- Wicker, B. *et al.* (2003) Both of us disgusted in My insula: the common neural basis of seeing and feeling disgust. *Neuron* 40, 655–664
- Keysers, C. *et al.* (2004) A touching sight: SII/PV activation during the observation and experience of touch. *Neuron* 42, 335–346
- Singer, T. *et al.* (2004) Empathy for pain involves the affective but not sensory components of pain. *Science* 303, 1157–1162
- Jackson, P.L. *et al.* (2005) How do we perceive the pain of others? A window into the neural processes involved in empathy. *Neuroimage* 24, 771–779
- Morrison, I. *et al.* (2004) Vicarious responses to pain in anterior cingulate cortex: is empathy a multisensory issue? *Cogn. Affect. Behav. Neurosci.* 4, 270–278
- Avenanti, A. *et al.* (2005) Transcranial magnetic stimulation highlights the sensorimotor side of empathy for pain. *Nat. Neurosci.* 8, 955–960
- Botvinick, M. *et al.* (2005) Viewing facial expressions of pain engages cortical areas involved in the direct experience of pain. *Neuroimage* 25, 312–319
- Preston, S.D. and de Waal, F.B.M. (2002) Empathy: its ultimate and proximate bases. *Behav. Brain Sci.* 25, 1–20
- Hoffman, M.L. (2000) *Empathy and Moral Development: Implications for Caring and Justice*. Cambridge University Press
- Hoffman, M.L. (2002) How automatic and representational is empathy, and why. *Behav. Brain Sci.* 25, 38–39
- Eisenberg, N. and Fabes, R.A. (1990) Empathy: conceptualization, measurement, and relation to prosocial behavior. *Motiv. Emot.* 14, 131–149
- Wispé, L. (1986) The distinction between sympathy and empathy: to call forth a concept, a word is needed. *J. Pers. Soc. Psychol.* 50, 314–321
- Brass, M. and Heyes, C. (2005) Imitation: is cognitive neuroscience solving the correspondence problem? *Trends Cogn. Sci.* 9, 489–495
- Keysers, C. and Perrett, D.I. (2004) Demystifying social cognition: a Hebbian perspective. *Trends Cogn. Sci.* 8, 501–507
- de Vignemont, F. (2006) When do we empathize? In *Empathy and Fairness N. 278* (Frith, C., ed.), John Wiley & Sons
- Eisenberg, N. and Strayer, J., (eds) (1987) *Empathy and Its Development*. Cambridge University Press
- Krebs, D. (1975) Empathy and altruism. *J. Pers. Soc. Psychol.* 32, 1134–1146
- Cialdini, R.B. *et al.* (1997) Reinterpreting the empathy–altruism relationship: when one into one equals oneness. *J. Pers. Soc. Psychol.* 73, 481–494
- Batson, C.D. *et al.* (2005) Similarity and nurturance: two possible sources of empathy for strangers. *Basic Appl. Soc. Psych.* 27, 15–25
- Avenanti, A. *et al.* (2006) Stimulus-driven modulation of motor-evoked potentials during observation of others' pain. *Neuroimage* 32, 316–324
- Singer, T. *et al.* (2006) Empathic neural responses are modulated by the perceived fairness of others. *Nature* 439, 466–469
- Lamm, C. *et al.* The neural substrate of human empathy: effects of perspective taking and emotion regulation. *J. Cogn. Neurosci.* (in press)
- Eisenberg, N. (2000) Emotion, regulation, and moral development. *Annu. Rev. Psychol.* 51, 665–697
- Baron-Cohen, S. and Wheelwright, S. (2004) The empathy quotient: an investigation of adults with Asperger syndrome or high functioning autism, and normal sex differences. *J. Autism Dev. Disord.* 34, 163–175
- Eisenberg, N. *et al.* (1995) Prosocial development in late adolescence: a longitudinal study. *Child Dev.* 66, 1179–1197
- Eisenberg, N. and Morris, A.S. (2001) The origins and social significance of empathy-related responding. A review of empathy and moral development: implications for caring and justice by M.L. Hoffman. *Soc. Justice Res.* 14, 95–120
- Nichols, S. *et al.* (1996) Varieties of off-line simulation. In *Theories of Theories of Mind* (Carruthers, P. and Smith, P., eds), pp. 39–74, Cambridge University Press
- Jacob, P. and Jeannerod, M. (2005) The motor theory of social cognition: a critique. *Trends Cogn. Sci.* 9, 21–25
- Friston, K.J. *et al.* (2003) Dynamic causal modeling. *Neuroimage* 19, 1273–1302
- Ochsner, K.N. *et al.* (2002) Rethinking feelings: an FMRI study of the cognitive regulation of emotion. *J. Cogn. Neurosci.* 14, 1215–1229
- Anderson, M.C. *et al.* (2004) Neural systems underlying the suppression of unwanted memories. *Science* 303, 232–235
- Blair, R.J. *et al.* (2005) *The Psychopath: Emotion and the Brain*. Blackwell
- Darwin, C. (1872, reprinted 1998) *The Expression of the Emotions in Man and Animals*, Oxford University Press
- Hamilton, W.D. (1964) The evolution of social behavior. *J. Theor. Biol.* 7, 1–52
- Perry, J. (2001) *Knowledge, Possibility and Consciousness*. MIT Press

- 37 Decety, J. and Jackson, P.L. (2004) The functional architecture of human empathy. *Behav. Cogn. Neurosci. Rev.* 3, 71–100
- 38 Keysers, C. and Gazzola, V. Towards a unifying neural theory of social cognition. *Prog. Brain Res.* (in press)
- 39 Hume, D. (1739-1740, reprinted 1978) *A Treatise of Human Nature* (2nd edn) (Selby-Bigge, L.A., ed.), Clarendon Press
- 40 Batson, C.D. and Shaw, L.L. (1991) Evidence for altruism: toward a pluralism of prosocial motives. *Psychol. Enquiry* 2, 107–122
- 41 Kennett, J. (2002) Autism, empathy and moral agency. *Philos. Q.* 52, 340–357
- 42 Lakin, J. and Chartrand, T.L. (2003) Using nonconscious behavioral mimicry to create affiliation and rapport. *Psychol. Sci.* 14, 334–339
- 43 Goldman, A. (1995) Empathy, mind and morals. In *Mental Simulation: Philosophical and Psychological Essays* (Davies, M. and Stone, S., eds), pp. 185–208, Blackwell
- 44 Ravenscroft, I. (1998) What is it like to be someone else? Simulation and empathy. *Ratio* 11, 170–185
- 45 Blakemore, S.J. *et al.* (2005) Somatosensory activations during the observation of touch and a case of vision-touch synaesthesia. *Brain* 128, 1571–1583
- 46 Gallese, V. (2003) The manifold nature of interpersonal relations: the quest for a common mechanism. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* 358, 517–528
- 47 Carr, L. *et al.* (2003) Neural mechanisms of empathy in humans: a relay from neural systems for imitation to limbic areas. *Proc. Natl. Acad. Sci. U. S. A.* 100, 5497–5502
- 48 Leslie, K.R. *et al.* (2004) Functional imaging of face and hand imitation: towards a motor theory of empathy. *Neuroimage* 21, 601–607
- 49 Meltzoff, A.N. and Decety, J. (2003) What imitation tells us about social cognition: a rapprochement between developmental psychology and cognitive neuroscience. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* 358, 491–500
- 50 Jackson, P.L. *et al.* (2006) Empathy examined through the neural mechanisms involved in imagining how I feel versus how you feel pain. *Neuropsychologia* 44, 752–761

Have you contributed to an Elsevier publication? Did you know that you are entitled to a 30% discount on books?

A 30% discount is available to all Elsevier book and journal contributors when ordering books or stand-alone CD-ROMs directly from us.

To take advantage of your discount:

1. Choose your book(s) from www.elsevier.com or www.books.elsevier.com

2. Place your order

Americas:

Phone: +1 800 782 4927 for US customers

Phone: +1 800 460 3110 for Canada, South and Central America customers

Fax: +1 314 453 4898

author.contributor@elsevier.com

All other countries:

Phone: +44 (0)1865 474 010

Fax: +44 (0)1865 474 011

directorders@elsevier.com

You'll need to provide the name of the Elsevier book or journal to which you have contributed. Shipping is free on prepaid orders within the US.

If you are faxing your order, please enclose a copy of this page.

3. Make your payment

This discount is only available on prepaid orders. Please note that this offer does not apply to multi-volume reference works or Elsevier Health Sciences products.

For more information, visit www.books.elsevier.com